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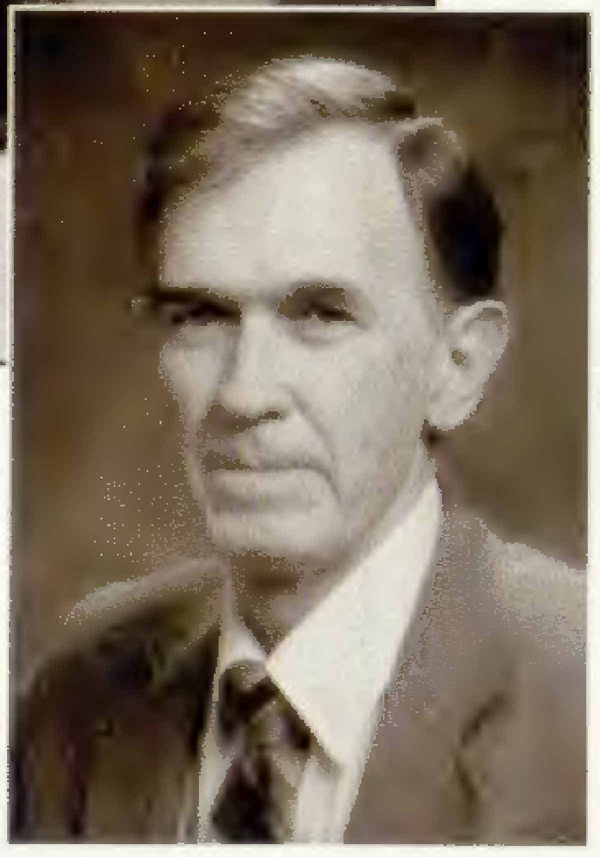

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Botanical Research Institute of Texas (BRIT)
509 Pecan Street
Fort Worth, Texas 76102-4060, USA

Editor

Barney L Lipscomb
Botanical Research Institute of Texas
509 Pecan Street
Fort Worth, Texas 76102-4060, USA
817-332-7432; 817-332-4112 fax
Electronic mail: barney@brit.org; jbrit@brit.org

Contributing Spanish Editor

Félix Llamas
Dpto. de Botánica, Facultad de Biologia
Universidad de Léon
E-2471 Léon, SPAIN

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Xyris panacea L.C. Anderson & Kral, sp. nov.—**1**

XYRIS PANACEA (XYRIDACEAE)—A NEW YELLOW-EYED GRASS FROM THE FLORIDA PANHANDLE

Loran C. Anderson

Professor Emeritus, Department of Biological Science
Florida State University
Tallahassee, Florida 32306-4370, U.S.A.

Robert Kral

Professor Emeritus, Vanderbilt University
1425 Pine Circle, N.W.
Cairo, Georgia 31728, U.S.A.

ABSTRACT

A new species of yellow-eyed grass (**Xyris panacea**) from depression ponds in the Big Bend area of the Florida panhandle (USA) is technically described, and comparisons are made to related species.

RESUMEN

Se describe una nueva especie de (**Xyris panacea**) de los estanques de depresiones en el área de Big Bend en la franja de Florida (USA) y se hacen comparaciones con las especies relacionadas.

An intensive plant survey by the senior author of the St. Marks National Wildlife Refuge included discovery of an unusual *Xyris* that in normal years would probably have been accessible only by boat, but the drought for the spring months of 2007 was the most severe on record for the Florida panhandle (USA). This enabled collecting the plants on foot—albeit I was up to my armpits in water on one occasion because at some sites the new *Xyris* grows on floating islands. The species description follows the format and terminology of Kral (2000).

Xyris panacea L.C. Anderson & Kral, sp. nov. (**Figs. 1–2**). Type: U.S.A. Florida. Wakulla Co.: St. Marks National Wildlife Refuge, common in mucky substrate and shallow water of "droughted" pond (East Renfro Lake) dominated by *Eleocharis equisetoides* and *Nymphaea odorata* near SE edge of Panacea Field, ca. 1.7 air mi SW of Panacea, Lat. 30.00742 N, Long. 84.42203 W, 23 Aug 2007, *L.C. Anderson 23,436* (holotype: FSU; isotypes: MO, NY, VDB).

Planta robusta, perennis, caespitosa, 7–10(–13) dm alta. Caules incrassati, varie elongati (basibus in substratio profundo elongati, ramificantes ascendentibus) cum (frequente) ascendentibus aut effusis stolones efferentibus. Folia pricinpalia rigid, disticha, anguste flabellate expansa, ca. 32–45(–50) cm longa, vaginis scaporum longiora; laminae planae vel leveter tortae, 3–5(–8) mm latae, compressae, 1–2.5-plo vaginis breviores, integrae, subtiliter multicostatae, virides; apices gradatim contracti, incurato-acuti; vaginae carinatae, carinibus integris, lateribus leviter multicostatis, glabris, rufobrunneolae aut brunneolae, maringibus integris, scariosis aut dilutis, in laminae gradatim convergentibuis, infimis gradatimexpensis, dilute brunneolis, leviter convexis, usque ad 1.5 cm latis. Vaginae scaportum a basin convolutae, acute unicarinatae, lamprobrunneolae, tortae, leviter multicostatae, laminis erectis, planis, usque ad 15 cm longis et 3 mm latis. Scapis gracilices, recti, apicem versus in sectio transversali elliptici, vulgo unicostati, ca. 1 mm crassi. Spicae anguste ovoideae vel agnuste ellipsoideae aut (vulgo) cylindricae, 2–4(–4.5) cm longae, obtusae, multibracteatae, bracteis sprialiter imbricatis, convexis, ecarinatis, late aut anguste obovatis. Bracteae steriles plures, fertilibus breviores in eas gradatim transientes, pari infima carinata aut ecarinata, rotundatis. Bracteae fertilies late aut anguste obovatae, 7–8 mm longae, rotundatae, lamprobrunneolae, areis dorsalis distinctis, late ovatis pallidis. Sepala lateralia libera, anguste oblanceolata, 7–8 mm longa, pallide brunneola; ala carinali super medium lacerociliata aut piloso ciliata. Laminae petalorum late obovate, 5 mm longae, apice late rotundatae, denticulatae. Staminodia bibrachiata, brachiis longipenicillatis. Antherae oblongae, ca. 2 mm longae, filiis ca. 0.5 mm longis. Capsulae anguste obovoideae, ca. 5 mm longae, dorsaliter convexae. Semina subcylindrica vel irregulariter ellipsoidea, 0.7–0.8 mm longa, translucida, brunneola, longitudinae valde multicostata et subtiliter transversilineata.

Robust, solitary to cespitose perennials 7–10(–13) dm long, the bases typically slightly bulbous, firm, buried in a mucky, often submersed, substratum, thus periodically producing (on larger plants) elongate ascending branches (internodes) and new "rosettes," the older, more basal nodes producing dense mats of pale, spongy roots, whereas new nodes produce spreading-arching stolons tipped with new plants. Principal leaves subdistichously in narrow fans, ca. 32–45(–50) cm long, longer than the scape sheaths, entire, multicostulate, green proximally shading to red, flat or slightly twisted, 3–5(–8) mm wide, 1–2.5 times shorter than the sheathes, gradually narrowed to incurved-acute tips; sheathes entire, narrowly convex at

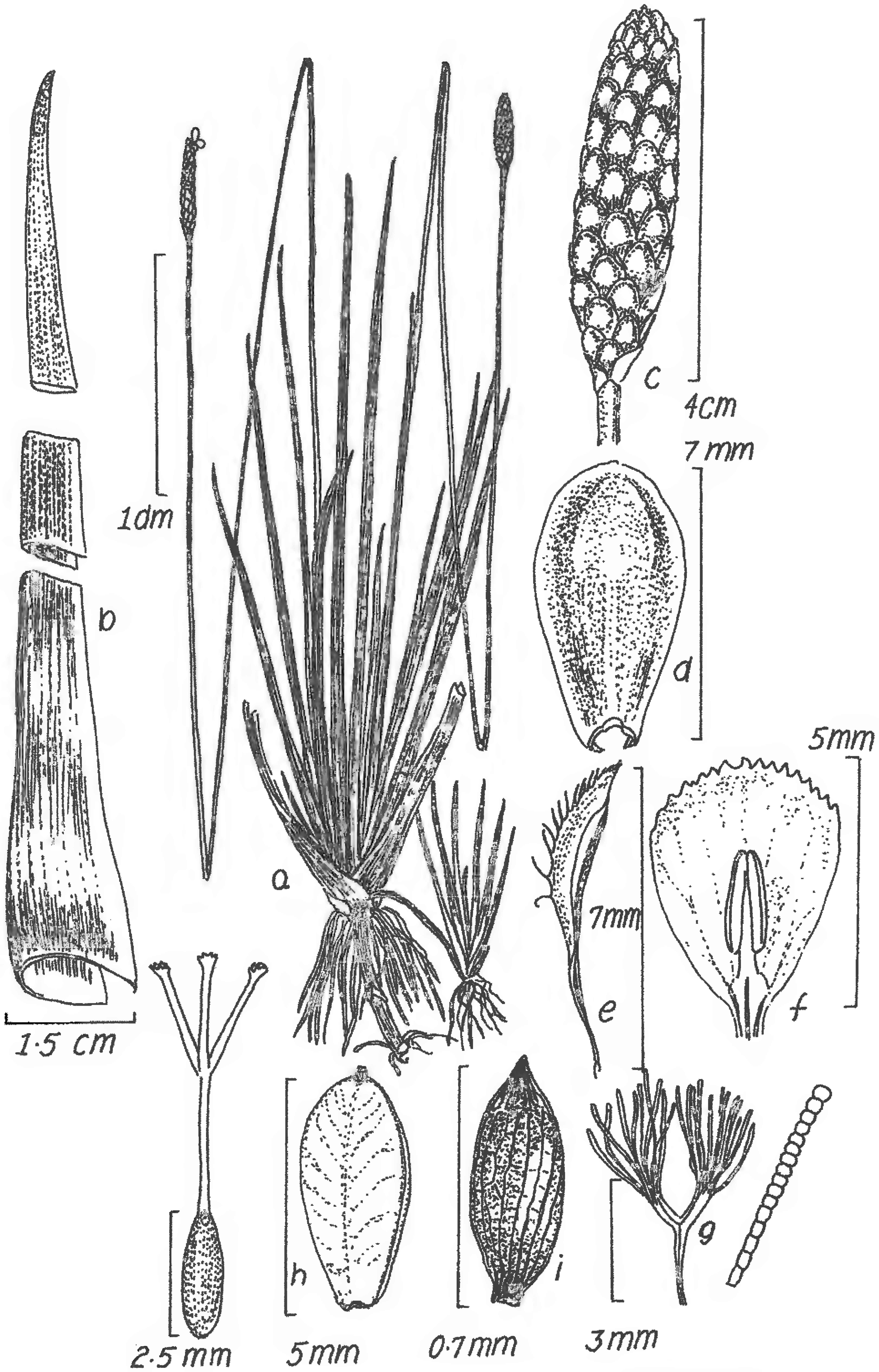

Fig. 1. ***Xyris panacea*** **(*Anderson 23438*). a. Habit sketch showing vertical rhizome-like stem and stolon. b. Leaf base, mid-sector, and apex. c. Spike. d. Fertile bracts. e. Lateral sepal. f. Petal blade, stamen (measurement taken by Kral from revived material; larger petals and stamens observed by Anderson from fresh material). g. Staminode (left); beard hair (right). h. Capsule (right); gynoecium at anthesis (left). i. Seed.**

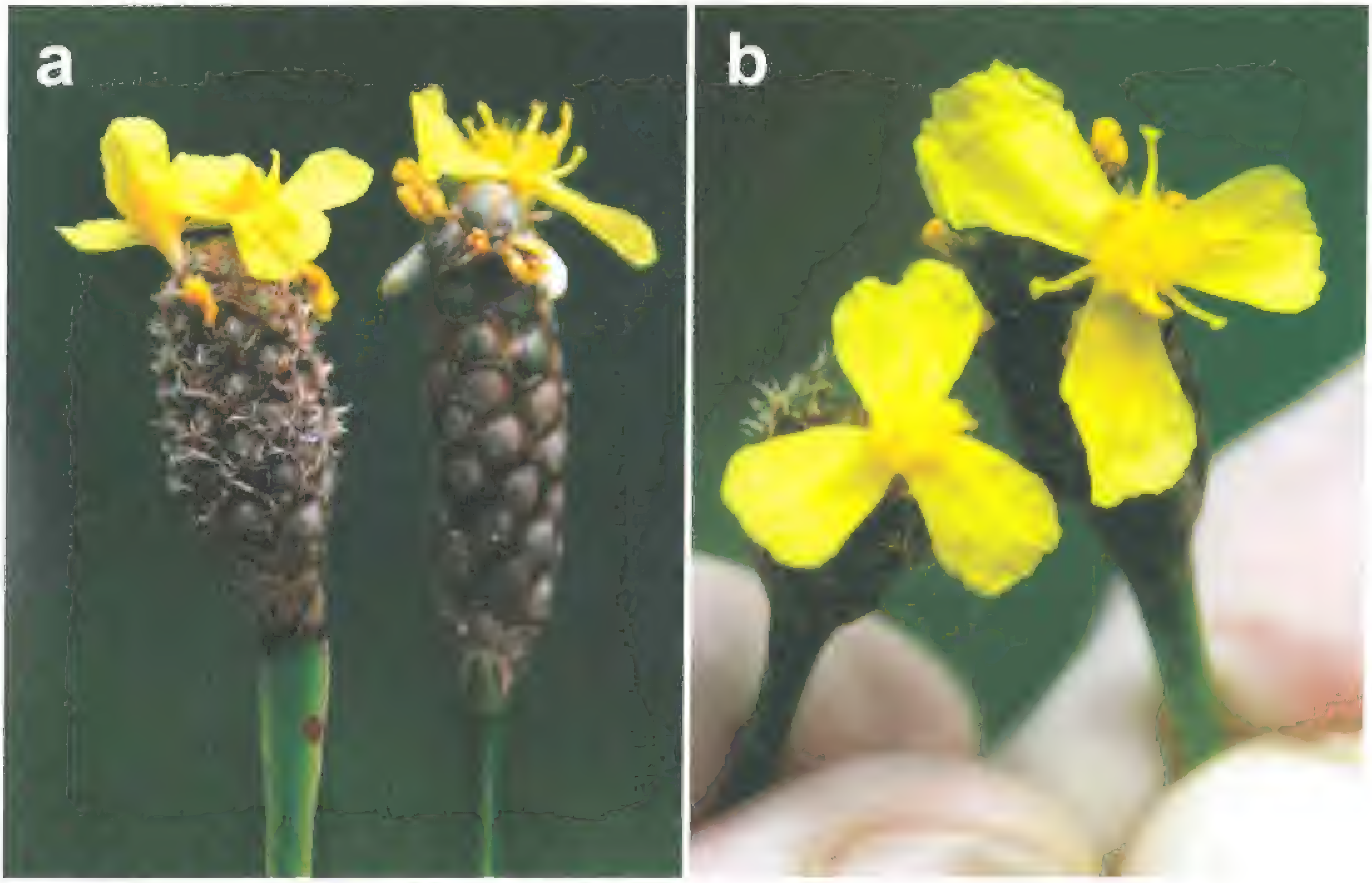

Fig. 2. Comparative digital photographs of *Xyris fimbriata* (*Anderson 23476*) and *X. panacea* (*Anderson 23477*) floral features, from transplanted plants. a. Lateral view of spikes and supporting scapes; *X. fimbriata* on left showing scape with scabrid ridges and spike with prominently exserted fimbriate sepals, *X. panacea* on right showing narrower, smooth scape and long, narrowly cylindric spikes with smaller exserted sepals. b. Distal views of flowering spikes; *X. fimbriata* on left with style branches hidden by the staminodia, *X. panacea* on right showing much larger petals and horizontally disposed style branches.

very base, there laterally 1–11.5 cm wide, lustrous dark red aging red-brown or deep brown, distally keeled, gradually narrowing into blade, reddish shading to green, eligulate. Scape sheaths shorter than principal leaves, proximally convolute, sharply keeled, lustrous brown or red-brown, twisted, shallowly multicostate, distally opening to an erect, keeled blade. Scapes slender, erect, 60–115(–130) cm long, red-brown shading to green distally, oval or elliptic in cross-section and 1–1.2 mm wide with one firm, smooth costa. Spikes usually narrowly cylindric, also narrowly ovoid to narrowly ellipsoid, 2–4(–4.5) cm. long, obtuse, multibracteate, the bracts imbricate in high spiral, convex, ecarinate (except sometimes with carinate basal pair), broadly to narrowly obovate, entire and distinct dorsal areas. Sterile bracts several, shorter than the fertile and grading into them; fertile bracts 7–8 mm, lustrous dark to pale brown, in contrast to the subapical, broadly ovate to elliptic, gray-brown to dark green dorsal areas. Lateral sepals free, narrowly oblanceolate, 7–8.5 mm long, inequilateral, the keel above middle (often) pilose, thence distally increasingly lacerociliate or pilose-ciliate, with tip acute and slightly to noticeably exserted. Petal blades broadly obovate, 8–9.5 mm long, 6–7 mm wide, apex shallowly rounded, denticulate. Staminodia 3–4.5 mm long, bibrachiate, branches elongate-penicillate. Anthers oblong, 2.5–3 mm long, on stout filaments 0.5–0.8 mm long. Styles 4.5–5 mm long, first ascending, then spreading horizontally between petals with age. Capsules narrowly obovoid, ca. 5 mm long, adaxial side plane, abaxial side convex; placentation 3-parietal. Seeds narrowly to broadly fusiform, 0.7–0.8 mm long, light brown, translucent, longitudinally strongly multiribbed with numerous finer, straight or diagonal connecting lines.

Etymology.—The specific epithet commemorates its geographical area (no curative powers are known).

Common name.—"St. Marks yellow-eyed grass" would be an appropriate common name.

Phenology.—Transplants of all relevant collections were potted in orginal substrate and cultivated in a flooded wheelbarrow in Anderson's backyard for observation. The new species blooms from late June to early October. Flower buds unfurl and petals are fully expanded around 11:30 am (EDT); in a close associate, *X. fimbriata* Elliott, the flowers open around 1:00 pm and stay open about two hours, whereas those of *X. panacea* remain open until around 4:00 pm. Flowers of *X. smallinana* Nash (in this region) open around 5:00 pm, and their flowering does not overlap with the other species. Flowering observations among the transplants were confirmed in the field.

Habitat.—The Refuge Comprehensive Conservation Plan (U.S. Fish and Wildlife Service 2006) lists ponds in the Panacea unit variously as "coastal depression ponds" or "basin lakes" or "flatwoods lakes." The St. Marks yellow-eyed grass grows either in mucky, loosely matted sandy loam in shallow depression ponds in longleaf pinewoods (with stems bases submerged in 10 or more centimeters of water or in poorly congealed loam of floating islands in those depression ponds (with stem bases only slightly submerged). Some ponds are ringed with a thicket of *Cyrilla racemiflora* L., whereas others are bounded by *Hypericum fasciculatum* Lam. The new species was vouchered from five ponds in the area; it is presumably present in several other ponds that Anderson planned to visit, but his 2007 field season was terminated abruptly with a broken leg.

Associated species.—Frequently seen taxa (other than other *Xyris*) at one or more sites include: *Bacopa caroliniana* (Walter) B.L. Rob. , *Burmannia biflora* L., *Cyrilla racemiflora*, *Decodon verticillatus* (L.) Elliott, *Drosera intermedia* Hayne, *Eleocharis baldwinii* (Torr.) Chapm., *E. elongata* Chapm., *E. equisetoides* (Elliott) Torr., *Eriocaulon compressum* Lam., *Fuirena breviseta* (Cov.) Coville, *F. scirpoidea* Michx., *Habenaria repens* Nuttall, *Hydrocotyle bonariensis* Comm. ex Lam., *Hypericum* fasciculatum, *Lachnanthes caroliana* (Lam.) Dandy, *Ludwigia alata* Elliott, *Lycopodiella appressa* (Chapm.) Cranfill., *Mayaca fluviatilis* Aubl., *Myriophyllum laxum* Shuttlew. ex Chapm., *Nuphar advena* (Aiton) W. Aiton ssp. *orbiculata* (Small) Padgett, *Nymphaea odorata* Sol., *Nymphoides aquatica* (J.F. Gmel.) Kuntze, *Panicum verrucosum* Muhl., *Pontederia cordata* L, *Rhynchospora careyana* Fernald, *R. cephalantha* A. Gray, *R. tracyi* Britton, *Sagittaria lancifolia* L., *Scleria reticularis* Michx., *Triadenum virginicum* (L.) Raf., *Utricularia floridana* Nash, *U. juncea* Vahl, and *U. purpurea* Walter.

Paratypes. *Anderson 23,437* (AUA, FLAS, FSU, GA, USF, VDB, VSC), *Anderson 23,438* (FLAS, FSU, GA, USCH, USF), *R. Kral 98,248* (VDB).

Additional collections (all **FLORIDA. Wakulla Co.:** St. Marks National Wildlife Refuge). East Renfro Lake near type locality, Lat. 30.00754 N, Long. 84.42194 W., 7 Aug 2007, *Anderson 23396* (FSU, VDB); "Point 4 Pond" (0.4 mi S of Otter Lake Rd on Refuge Rd 319), Lat. 30.02258 N, Long. 84.40673 W, 4 Sep 2007, *Anderson 23473* (FSU); "Point 8 Pond" (0.8 mi S of Otter Lake Rd on Refuge Rd 319), Lat.30.01715 N, Long. 84.40813 W, 4 Sep 2007, *Anderson 23477* (AUA, FSU, VDB); pond W side Rte 372 (opposite Refuge Rd 334), Lat.30.02234 N, Long. 84.44504 W,11 Sep 2007, *Anderson 23502* (FSU, MO, NY); floating island in North Lake, S of Refuge Rd 329, SW of Otter Lake, Lat.30.01434 N, Long. 84.42978 W, 25 Sep 2007, *Anderson 23595* (FLAS, FSU, FTG, GA, MO, UNA, VSC).

DISCUSSION

The common associate *Xyris* in these ponds is *X. fimbriata*, a species of similar habit and pigmentation but with two scabrid scape costae (rather than a single, smooth one), with spikes mostly shorter and of broader outline, with lateral sepals strongly exserted, their keels densely fimbriate (Fig. 2). Also, a few diminutive flowering plants of *X. jupicai* L. Rich. were seen at the type locality. Ponds 3.8 km and 4.3 km NE of the new taxon's range had the "*X. panacea* zone" replaced with *X. smalliana* exclusively; see *Anderson 23456, 23457* (FSU, VDB). In the general area, though not an associate, is *X. stricta* Chapm., another tall species with similarly ascending, long-sheathed, slender-bladed leaves and similar pigmentation. This taxon also has narrowly ellipsoidal to subcylindric spikes with similar design of bracts. However, this taxon has scapes distally broader, flatter, actually 2-edged, its lateral sepals are broader, with broader, firmer, ciliolate keels whose tips are not exserted; its seeds are typically farinose.

The St. Marks yellow-eyed grass is distinctive with a suite of vegetative and floral features. The dark red stem bases are somewhat bulbous and firm (being pale green and soft in X. *fimbriata* or pale green and

mucilagionous in *X. smalliana*); larger plants have stout vertical, rhizome-like stems and more delicate stolons. The flowering scapes are smooth with weakly developed ribs below the spikes. The spikes are cylindric, longer than those of any other taxa in North America (Kral 2000). Flowers open earlier in the day and are larger than those of other species (equally large petals are found in *X. caroliniana* Walter, but that species differs in habitat and very many aspects of morphology). More attention needs to be given to style position amongst North American species; the horizontally spreading style branches in *X. panacea* may be exclusively unique. The known range of the new species is sufficiently small to warrant designating it a threatened or endangered species.

ACKNOWLEDGMENTS

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BOOK REVIEW

Harry S. Paris. **The Drawings of Antoine Nicholas Duchesne for his Natural History of the Gourds.** (ISBN 9782856536049, hbk.). Muséum National d'Histoire Naturelle, Publications Scientifiques, Diffusion 57 Rue Cuvier, F-75231 Paris Cedex 05, France. (**Orders:** www.mnhn.fr/publication, diff.pub@mnhn.fr, 33 (0)1 40 79 48 05). $257.00, 454 pp., 258 color plates, 17 1/2" × 12 3/4".

French horticulturalist and botanist Antoine Nicholas Duchesne (1747–1827) was born at Versailles. Duchesne became a careful observer of nature under the tutelage of his scholarly and well-traveled father, and later under Bernard de Jussieu (the second of the five de Jussieus of botanical history) at the King's Garden in Paris, who was himself tutored by Linnaeus. Duchesne corresponded with Linnaeus on botanical matters, particularly on his first interest, in the relationships and hybridization of strawberries. Though it was unusual at the time for a botanist to restrict himself to in-depth studies of the type that we now call monography, in one of his letters to Duchesne, Linnaeus said, "When you have completed the history of the wild strawberries, you will have accomplished something which I long have hoped that some botanists would do; namely, that they would each choose their plant family and examine it most thoroughly; in this manner would soon be attained the ultimate knowledge of plants which now floods botanists with its abundance."

Duchesne's first work, *L'Histoire naturelle des frasiers (Natural history of the strawberries)*, was published in 1766 when he was only 19 years old. One product of this research included his own botanical illustrations, in pencil and ink (though he lacked the funds to see them published in his lifetime). Duchesne was particularly interested in plant sexual systems as they pertained to the creation of domesticated plants, and through cross-pollination experiments he developed (and attempted to retrace the parentage of) various strawberry cultivars. His experiments led him to the idea of what we now call the biological species concept, a refutation of the doctrine of constancy or immutability of species as maintained by other naturalists of his era. He called himself a "cultivator botanist," distinct from other botanists who observed without experimentation. After all, this was the Age of the Enlightenment.

His next major work focused on pumpkins, squash, and gourds of the genus *Cucurbita*. All *Cucurbita* species arose in the New World and thus only became known to Europeans after 1492. Initially the various species and cultivars of *Cucurbita pepo* were grown in Europe for ornamental interest only, but over time many more were developed that were more palatable and better suited to the long day lengths of northern summers. Duchesne was drawn to *Cucurbita* for its incredibly varied fruit characteristics (pleasing to the eye and hand of a botanical artist), but he also found this to be a genus perfectly suited to more cross-breeding experiments, and a similar mystery of origins of forms, recalling his first love of strawberries.

Most of Duchesne's writing and illustrations produced from this period did not come to light until recently, and in this book his entire collection of illustrations of *Cucurbita* is published for the first time. The author Dr. Harry Paris, one of the foremost experts on *Cucurbita*, is responsible for finally locating Duchesne's rumored illustrations in the Library of the Natural History Museum in Paris. Contained in this massive tome (falling somewhere between a folio and elephant folio at 44.5 cm in length and weighing approximately 6 kg) are 361 of Duchesne's illustrations, mostly of those cultivars commonly called gourds. These illustrations include pencil sketches and pen-and-ink works but the majority are full-color watercolors (258 color plates). The primary focus is on the form and color patterns of fruits, and their textures, with a loving attention to warty protrusions of all kinds. Since this book is gigantic, many of these illustrations approach life-size. The works range from hazy impressionistic arrangements to startlingly photo-realistic pieces worthy of any Dutch Master's still life. Included here too are a number of Duchesne's illustrations of *Cucurbita* flowers and their developmental stages, and pencil studies of the growth patterns of the vines, which are more delicate works in general.

Also included are a number of brief yet substantial chapters (in both English and French) interpreting the biography of Duchesne and botanical significance of his work, as well as a chapter on the botany of the genus *Cucurbita*, and a glossary and index to scientific names. This is the *sine qua non* coffee table book for any fan of cucurbits, horticulture, or botanical illustration, but with the interpretive chapters bookending the illustrations, this book is also of significance and utility to systematists.—*Amanda K. Neill, Director of the Herbarium (BRIT-SMU-VDB), Botanical Research Institute of Texas, 500 East 4th Street, Fort Worth, Texas 76102-4025, U.S.A.*

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MOLECULAR ANALYSIS OF SOLIDASTER CV. LEMORE, A HYBRID GOLDENROD (ASTERACEAE)

Edward E. Schilling
Department of Ecology and Evolutionary Biology
University of Tennessee
Knoxville, Tennessee 37996, U.S.A.
author for correspondence (eschilling@utk.edu)

James B. Beck
Department of Biology
Washington University, Campus Box 1137
St. Louis, Missouri 63130, U.S.A.
and Missouri Botanical Garden
St. Louis, Missouri 63136, U.S.A.
Current address: Department of Biology
Duke University, Durham North Carolina 27708, U.S.A.

Patrick J. Calie
Department of Biological Sciences
Eastern Kentucky University
Richmond, Kentucky 40475, U.S.A.

Randall L. Small
Department of Ecology and Evolutionary Biology
University of Tennessee
Knoxville, Tennessee 37996, U.S.A.

ABSTRACT

Analysis of nuclear ribosomal ITS and ETS sequence data was used to assess the relationships of the garden ornamental Solidaster cv. Lemore, a cultivar that was at one time believed to be an intergeneric hybrid (*Solidago* × *Aster*). Part of the analysis involved assessment of the generic placement of one of its putative parents, the Upland White Aster, *Solidago ptarmicoides*. Because of its superficial external appearance this species is still often treated as an *Aster*, although there is evidence from several sources that suggests it should be classified within *Solidago*. Phylogenetic analysis of the combined ITS and ETS sequence data showed that there was strong support for the inclusion of *S. ptarmicoides* within *Solidago*, based on its placement in a well supported clade composed of all other sampled species of the genus. The ITS sequence data of Solidaster showed evidence of a hybrid origin based on the presence of several intraindividual base pair polymorphisms. Cloning experiments recovered two different individual ITS sequences, one identical to that obtained from *S. ptarmicoides* and a second that matched sequences obtained for *S. canadensis*. Thus DNA sequence data suggested that Solidaster cv. Lemore is a hybrid goldenrod that involved a cross between *S. ptarmicoides* and *S. canadensis*. The data further indicated that another possible candidate, *Euthamia graminifolia*, is not a parent of Solidaster. Also notable was the striking lack of sequence divergence for ITS and ETS among species of *Solidago*, suggesting that estimation of phylogenetic relationships within the genus will require more rapidly evolving markers.

Key Words: Asteraceae, Astereae, Solidaster, *Solidago*, ITS, ETS, hybrid, phylogeny

RESUMEN

Se realizó un análisis con los datos de las secuencias del ITS y ETS nuclear ribosómico para evaluar las relaciones de la planta ornamental Solidaster cv. Lemore, un cultivar que durante un tiempo se creyó que era un híbrido intergenérico (*Solidago* × *Aster*). Parte del análisis implicó la evaluación de la colocación del género de uno de los padres putativos, *Solidago ptarmicoides*. Debido al parecido externo de esta especie esta especie se trata a menudo como un *Aster*, aunque hay pruebas de varias fuentes que sugieren que debería clasificarse en *Solidago*. El análisis filogenético de datos combinado de las secuencias de los ITS y ETS mostró que hay un respaldo fuerte para la inclusión de *S. ptarmicoides* en *Solidago*, basado en su colocación en un clado bien respaldado compuesto por todas las otras especies muestreadas del género. Los datos de la secuencia del ITS de Solidaster mostraron pruebas de un origen híbrido basado en la presencia de varios polimorfismos de pares intraindividuales. Los experimentos de clonación recogieron dos secuencias de ITS individuales diferentes, una idéntica a la obtenida a partir de *S. ptarmicoides* y la segunda que coincidía con secuencias obtenidas de *S. canadensis*. Por tanto los datos de la secuencia de DNA sugieren que Solidaster cv. Lemore es una vara de oro híbrida procedente de un cruce entre *S. ptarmicoides* y *S. canadensis*. Los datos indicaron además que otro candidato posible, *Euthamia graminifolia*, no es un parental de Solidaster. Fue también notable la falta de divergencia en la secuencia de ITS y ETS entre especies de *Solidago*, sugiriendo que la estimación de relaciones filogenéticas requerirá marcadores de evolución más rápida.

INTRODUCTION

Consideration of the role of hybridization in evolution has received new impetus with the availability of molecular genetic data (Arnold 2006). It has long been clear that interspecific hybridization is a widespread

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phenomenon in plants, with numerous clearly documented examples (e.g., Grant 1980), but there are still questions regarding its evolutionary significance. Of perhaps greatest interest is hybridization between species of lineages that have diverged morphologically to the point of being recognized as distinct genera. This represents a potentially dramatic reversal of the process of evolution, which is normally considered to be divergent, and it also presents a challenge to systematic classification based on phylogeny. It is thus of considerable interest to examine closely possible cases of intergeneric hybridization to be able to assess how frequently this phenomenon occurs.

A persistent myth is that intergeneric hybridization is common and perhaps even pervasive within Asteraceae. For example, Robinson (1983) and King and Robinson (1987) invoke intergeneric hybridization as an explanation for discordant distribution of morphological characters in Liabeae and Eupatorieae, respectively. A search of the literature, however, reveals few well documented cases of natural intergeneric hybridization in Asteraceae. Naturally occurring intergeneric hybrids have recently been documented by McKenzie et al. (2004) and Saito et al. (2006). In some cases, artificial intergeneric hybrids have been made successfully (e.g., Powell 1985; Carr 2003), and studies have found incongruence between nuclear and chloroplast markers suggestive of past wide hybridization (Schilling & Panero 1996; Fehrer et al. 2007). But documentation of intergeneric hybrids in most groups remains elusive. This prompted us to undertake a detailed study of a putative case of intergeneric hybridization within the Astereae.

The name of the horticultural plant known as Solidaster cv. Lemore (Fig. 1) reflects its presumed hybrid origin as a cross between species of *Solidago* L. and *Aster* L. The plant is unknown in the wild, but appeared in European gardens after the import of plants from North America (Nesom 1993). Its status as an intergeneric hybrid depends in part, however, on the classification of one of its putative parents, the Upland White Aster, which has been variously placed in *Aster*, *Solidago*, and *Oligoneuron* Small. The Upland White Aster, *S. ptarmicoides* (Torrey & A. Gray) B. Boivin, has long been a source of puzzlement for taxonomists. Its superficial outward appearance, especially its open corymbose capitulescence and relatively large heads with white rays and disk flowers, seems clearly that of an aster, as traditionally conceived, and is reflected in its common name. Despite this, considerable evidence has suggested a closer affinity to the goldenrods, including the observation of abundant natural hybrids with species of *Solidago* (Boivin 1972), considerations of phytogeography and technical features of morphology (Brouillet & Semple 1981), and a chloroplast DNA restriction site study placing it within *Solidago* L. (Semple et al. 1999). Nevertheless, it is still widely referred to as an *Aster* s.l. Another, somewhat different interpretation involves segregation of the genus *Oligoneuron* as distinct from *Solidago* (e.g., Nesom 1993), which would include the Upland White Aster as well as five other species. Although the second parent of Solidaster has generally been considered to be a *Solidago*, particularly *S. canadensis* (Brouillet & Semple 1981), Nesom (1993) suggested that based on morphology it was more likely to be *Euthamia graminifolia* (L.) Nutt.

The taxonomic history of the Upland White Aster, *Solidago ptarmicoides*, has been reviewed by Brouillet and Semple (1981), and only a brief summary will be presented here. Not only the generic placement but also its species epithet has varied. The plant was originally described by Nuttall in *Inula* L., where it received the appropriate epithet *alba* for its white rays and disk flowers. When transferred to either *Aster* or *Solidago* this epithet proved to be already occupied, and the alternative *ptarmicoides* (from its resemblance to *Achillea ptarmica* L., a widely cultivated garden plant; Fernald 1950) was proposed by Nees. When placed in still another genus, such as *Oligoneuron* (e.g., Nesom 1993), it reverts to the epithet *album*. Over its taxonomic history, the species has been placed in nine separate genera by various authors (Semple & Cook 2006).

The taxonomic treatment of *Solidago* has been notoriously difficult (Semple & Cook 2006). Although there are a large number of relatively similar species in eastern North America, no clearcut morphological apomorphy has been discovered that unequivocally defines the genus. Similarly, delimitation of infrageneric groups has been elusive as has recognition and identification of individual species, many of which differ from one another by minute details of inflorescence form or pubescence. The situation is further complicated by the frequent occurrence of both interspecific hybridization and polyploidy. Some representatives

FIG. 1. Solidaster cv. Lemore, habit and close up of inflorescence.

of the genus are quite common and widespread and are particularly significant as dominants during early successional stages of old fields, where several are components of a well studied ecological model system (e.g., Abrahamson et al. 2005). Additionally, *Solidago* taxa have become invasive in Europe (Weber 2001) and Asia (Dong et al. 2006), and are being used as models to understand the general evolution and ecology of invasive species (Van Kleunen & Schmidt 2003; Jakobs et al. 2004; Meyer et al. 2005). The abundance and ecological importance of *Solidago* therefore make a sound taxonomy highly desirable.

A number of studies have applied molecular data to the resolution of systematic problems in Astereae (Suh & Simpson 1990; Morgan & Simpson 1992; Lane et al. 1996; Zhang 1996; Noyes & Rieseberg 1999; Roberts & Urbatsch 2003; Urbatsch et al. 2003; Beck et al. 2004), so a considerable body of molecular data has begun to accumulate for the tribe. Other than a chloroplast DNA restriction site analysis (Zhang 1996; Semple et al. 1999), there has been no focus as yet for DNA sequence analysis on *Solidago*, although a few sequences are available from other work. As part of an initial survey for suitable molecular markers, we analyzed ITS and ETS sequence variation for several samples of *Solidago* that represented the major subunits of the genus, as delimited by Semple and Cook (2006). Although the lack of suitable variation in these markers led us to abandon any attempt to make a complete survey of the genus, one of the species that we sampled was *S. ptarmicoides*, and sufficient data have been acquired to allow for an assessment of its generic placement, as well as to clarify the parentage of its hybrid offspring, Solidaster cv. Lemore, which we report here.

MATERIALS AND METHODS

Plant Material

A sample of Solidaster cv. Lemore (Fig. 1) was grown from material obtained commercially (Bluestone Perennials, Ohio, USA). Samples of *Solidago* (Appendix) were either collected in the field or obtained from herbarium specimens. Sampling was designed to include at least one member of each of the currently recognized sections and subsections of the genus (Semple & Cook 2006). To evaluate intraspecific variability, multiple accessions of four species (*S. canadensis*, *S. riddellii*, *S. ptarmicoides*, and *S. nitida*) as well as an additional sample of *Brintonia discoidea* were analyzed. Note that we have elected to follow the most recent treatment of *Solidago* (Semple & Cook 2006), which deviates from nomenclature used in our earlier paper

(Beck et al. 2004) by including *Oligoneuron* within *Solidago* but recognizing *Brintonia* as separate from it; the classification of related genera also follows the Flora of North America treatments.

Molecular Methods

Preparations of total DNA made from fresh (0.5–2.0 g) leaves generally followed the procedure of Doyle and Doyle (1987), and those from herbarium material (ca. 0.1 g) were performed with the Dneasy Plant Minikit (Qiagen, Valencia CA). The crude DNA extracts of some samples required further purification using the Wizard Kit protocol (Promega, Madison, Wisconsin). Methods for DNA amplification and sequencing were as described in Schmidt and Schilling (2000). Amplification and sequencing reactions for the ITS region were both performed using primers "ITS-4" and "ITS-5" (White et al. 1990). Amplification and sequencing reactions for the ETS region were performed using primers Ast-1 (Markos & Baldwin 2001) and 18-S-ETS (Baldwin & Markos 1998). All PCR products were checked by agarose gel electrophoresis. Sequencing was done at the University of Tennessee Automated Sequencing Facility, utilizing the ABI Prism Dye Terminator Cycle Sequencing reaction kit on an ABI 373 or ABI 3100 DNA sequencer (Perkin-Elmer Inc. Foster City, CA). The initial sequence data text files were edited following comparison with the same data displayed in four-color electropherograms before further analysis. Sequence alignment was performed using the Clustal X (version 1.6) program (Thompson et al. 1994).

Cloning of the ITS region for the sample of Solidaster cv. Lemore was undertaken to confirm ITS polymorphisms inferred from direct sequencing. The purified PCR products were ligated into pGEM-T (Promega, Madison, Wisconsin) according to the manufacturer's instructions. Competent Top10 F' (Invitrogen, San Diego, California) cells were transformed via electroporation and the resulting colonies were screened for plasmids with inserts by PCR using the original amplification primers. Plasmids were isolated from single recombinant colonies using an alkaline lysis/PEG precipitation protocol (Sambrook et al. 1989). Sequences were obtained for ten independent clones.

Data for additional ITS and ETS sequences for *Solidago* were obtained from GenBank, as well as for all of the samples placed in the same clade as *Solidago* s.s. in Beck et al. (2004; "Clade III"). Two data sets were analyzed, the first of which utilized ITS sequences from a broad sampling of *Solidago*, with samples of *Brintonia discoidea* as outgroups. The second utilized both ITS and ETS data with a broader sampling of related genera (Appendix) to assess the placement of *Solidago ptarmicoides* and of *Oligoneuron* relative to other *Solidago*, and samples of *Sericocarpus tortifolius* and *Cuniculotinus gramineus* were added as outgroups for this analysis. Phylogenetic relationships were analyzed using both maximum parsimony and Bayesian approaches. Parsimony analysis was implemented using PAUP* 4.0b10 (Swofford 2003), with gaps treated as missing data, using a heuristic search with 1,000 random addition replicates and with TBR branch swapping. Bootstrap analysis (Felsenstein 1985) was performed with 10,000 replicates using the FASTSTEP search option. Bayesian analysis was implemented in MRBAYES 3.0B4 (Huelsenbeck & Ronquist 2001) run for ten million generations with four separate chains and trees saved every 100 generations. The number of trees to discard as "burn-in" was assessed by plotting likelihoods of trees sampled throughout the run and discarding all trees prior to the stable likelihood plateau (in both analyses the first 10% were discarded). An appropriate maximum likelihood model of sequence evolution (GTR+I+G; General Time Reversible model with a proportion of invariant sites and gamma distributed rates) for the Bayesian analysis was chosen for both analyses using Modeltest (Posada & Crandall 1998).

RESULTS

Newly obtained ITS sequences for Solidaster cv. Lemore and for *Solidago* were consistent in length with previous reports for the genus. In particular, there was extraordinarily little variation in length among any of the sampled members of the genus; individual sequence lengths varied from 627–629 bp. Insertion of single 1 bp indels were required for five samples (three insertions and two deletions) to produce a completely aligned matrix of length 631 bp for the entire ITS region. Similarly, there was little sequence length variation in allied genera, with individual sequences varying from 627–630 bp, and the aligned matrix was of

length 634. There was also only limited sequence variation between species of *Solidago* for the ITS region; pairwise comparisons revealed sequence divergence of generally less than 1%, with total differences between samples of 1–10 bp. Samples of other genera were generally, although not always, more divergent, with pairwise divergence values of 1–3% and total differences of 7–19 bp. The sample of *Sericocarpus tortifolius* differed from all *Solidago* samples for at least 15 bp, but was still relatively similar, with overall divergence values of 2–3%; the sample of *Cuniculotinus gramineus* was somewhat more divergent, differing by 23–29 bp (4% overall divergence) from samples of *Solidago*. In the five species (*S. canadensis*, *S. riddellii*, *S. nitida*, *S. ptarmicoides*, and *Brintonia discoidea*) where multiple accessions were examined there was at most one bp difference among samples and no evidence of nonmonophyly.

The ITS sequence for Solidaster cv. Lemore was very similar to other *Solidago* sequences, but displayed bp polymorphisms (Fig. 2) at the following positions: 18 (A/G), 106 (C/A); 514 (C/T), 611 (G/T), 612 (C/T), 613 (A/G). Visual inspection revealed that this pattern of bp polymorphisms would fit exactly with a combination of the ITS sequences characteristic of *S. ptarmicoides* and *S. canadensis* (Fig 2.) Cloned ITS repeats from Solidaster cv. Lemore exhibited ITS sequences that matched closely either those of *S. ptarmicoides* or those of *S. canadensis*. Phylogenetic analysis in comparison to a broad sampling of *Solidago* showed that consensus sequences from the clones clustered with some statistical support with those from *S. ptarmicoides* and *S. canadensis* (Fig. 3), which provided supporting evidence that the polymorphisms obtained from direct sequencing could have originated from a combination of the sequences from these species. The ITS sequence of *Euthamia graminifolia*, proposed by Nesom (1993) as the second potential parent of Solidaster, has been shown to be relatively divergent from those of *Solidago* (Noyes and Rieseberg 1999), and its reported ITS sequence (GenBank AF046982) differs from that of *S. ptarmicoides* by 4 indels as well as a minimum of 32 bp. Because the ITS sequence of Solidaster cv. Lemore did not show any evidence of indel polymorphisms, and only a few bp polymorphisms, *Euthamia graminifolia* is clearly not one of its parents.

Approximately 450 bp of the ETS region were amplified for each sample of *Solidago* with the primer pair 18S-ETS and Ast-1. Removing regions of poor sequence and uncertain alignment produced a matrix with a total length of 444 bp, including 18 bp of 18S coding sequence. As with ITS, length variation among sequences was minimal among *Solidago* samples: only a single 1 bp deletion in *S. patula*, and only a single 1 bp insertion in *Stenotus* and a 3 bp deletion in both outgroup taxa, *Cuniculotinus* and *Sericocarpus*, were required for complete alignment of this portion of the ETS region. Levels of sequence divergence for ETS were similar to those for ITS, with pairwise divergence values among *Solidago* samples of 0–1% (0–4 bp) and among all samples reaching a maximum of 4% (17 bp). The ETS sequence of Solidaster cv. Lemore was basically identical to that of *S. ptarmicoides*, although each sequence exhibited a single, non-informative bp polymorphism (position 124 in Solidaster, 36 in *S. ptarmicoides*; both A/G). Other than the polymorphic positions, the ETS sequence of *S. canadensis* differed from those of *S. ptarmicoides* at only a single position, and there was no evidence of polymorphism in the sequence of Solidaster cv. Lemore at this position.

For phylogenetic analysis to assess the placement of *S. ptarmicoides* relative to *Solidago*, the ITS and ETS sequence data were analyzed together, producing a combined matrix of 1078 bp in which there were 46 potentially parsimony-informative characters and 85 additional variable but parsimony-uninformative characters. The results of phylogenetic analyses (Fig. 4) reflected the overall low levels of divergence in providing a poorly resolved tree with relatively low levels of support for many branches. The results of the parsimony and Bayesian analyses were topologically consistent although the Bayesian tree was more resolved. A monophyletic group corresponding to clade III of Beck et al. (2004) was defined relative to *Cuniculotinus gramineus* and *Sericocarpus tortifolius* with a posterior probability of 1.00 (Bayesian) and 100% (bootstrap), respectively. At the next level of branching there was a large polytomy in the strict consensus tree, within which there was a strongly supported clade formed by the three species of *Chrysothamnus*, *C. scopulorum*, *C. stylosus*, and *C. viscidiflorus* (1.00; 99%), a variably supported clade with *Petradoria* and *Stenotus* (0.97; 57%), and a strongly supported clade formed by *Solidago*, *Chrysoma*, and *Brintonia* (1.00; 76%). Within the last clade, there was a *Chrysoma* + *Brintonia* clade (0.79; <50%) that was sister to a *Solidago* s.s. clade (1.00; 69%). Within the *Solidago* s.s. clade, there was little resolution in the consensus tree, with the only bootstrap

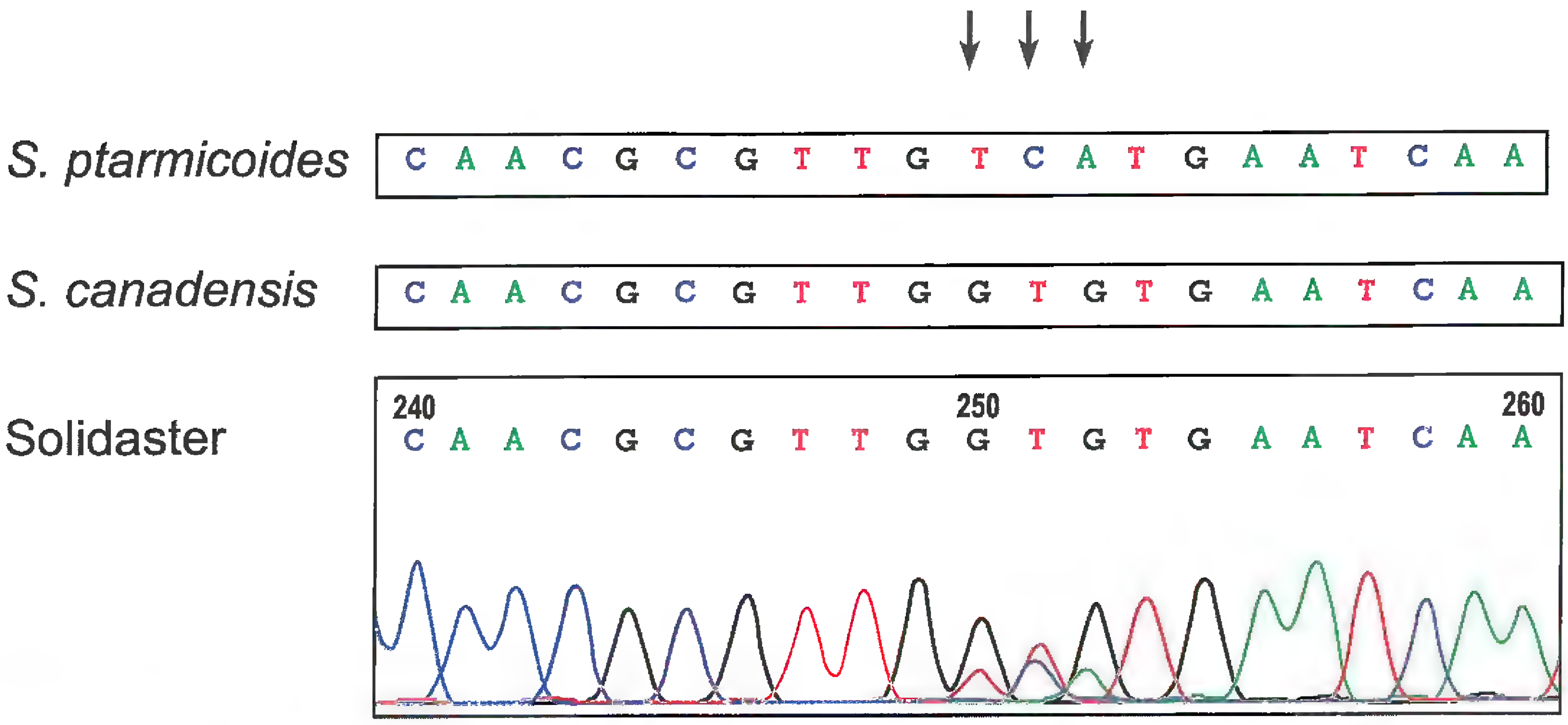

Fig. 2. Portion of an electropherogram showing base pair polymorphisms (arrows) in a portion of the ITS-2 region of Solidaster cv. Lemore compared to its putative parents, *S. canadensis* and *S. ptarmicoides*.

support greater than 80% for multispecific clades going to a strongly supported *S. canadensis* + *S. gigantea* clade (1.00; 94%); weaker support was provided to clades consisting of *S. rigida* + *S. ohiensis* (0.99; 64%), *S. caesia* + *S. riddellii* (0.62; 64%), and *S. arguta* + *S. patula* (0.50; <50%). The three samples of *S. ptarmicoides* were placed in a large polytomy with other members of the genus (Fig. 4). Results of the Bayesian analysis also provided weak to strong support for clades that received less than 50% bootstrap support, including *Petradoria/Stenotus* with *Solidago/Chrysoma/Brintonia* (0.94) and clades not present in the strict consensus tree: *Oreochrysum* + *Tonestus* (0.51), with sequential addition of *Lorandersonia* (0.52), and *Eastwoodia* (0.76), and this clade combined with the three species of *Chrysothamnus* (0.60). These results are completely congruent with those presented by Urbatsch et al. (2003) in placing *Oligoneuron* within *Solidago* as well as showing *Chrysoma* as a near outgroup to *Solidago* relative to *Sericocarpus*. They also support the revised classification of *Chrysothamnus* and related genera presented by Urbatsch et al. (2005).

DISCUSSION

Molecular data showed that Solidaster cv. Lemore is not an intergeneric hybrid by providing evidence not only to identify its parents (Figs. 2, 3) but to show clearly that both are accurately placed as members of *Solidago* (Figs. 3, 4). The combination of *Solidago ptarmicoides* and *S. canadensis* as its progenitors fits well with what is known of the origin of Solidaster, and has been proposed previously (e.g., Brouillet & Semple 1981). It has been clear based on morphology that *S. ptarmicoides* was one of the parents, and *S. canadensis* was one of the few goldenrod species naturalized near the nursery where Solidaster was first discovered (Nesom 1993). Although Solidaster does not show complete additivity in morphological features relative to *S. ptarmicoides* and *S. canadensis* (Nesom 1993), there are now numerous well documented cases of hybrids failing to exhibit one or more seemingly characteristic traits of their progenitors (Rieseberg 1995). Note that these results apply specifically to the cultivar Lemore, and other material marketed as "Solidaster" (or in florists shops as "Aster"), which may exhibit somewhat different morphologies, may not have a common origin. Laureto and Barkmann (2005, pers. comm.) present molecular-based evidence for the hybrid origin of another species, *S. houghtonii* Torr. & A. Gray ex A. Gray, that involves members of sect. *Ptarmicoidei* (*S. riddellii*) and sect. *Triplinerve* (*S. gigantea*), and similarly does not show additivity in morphology. Exclusion of *Euthamia graminifolia* as a potential parent of Solidaster also refutes another potential intergeneric hybridization hypothesis (Nesom 1993).

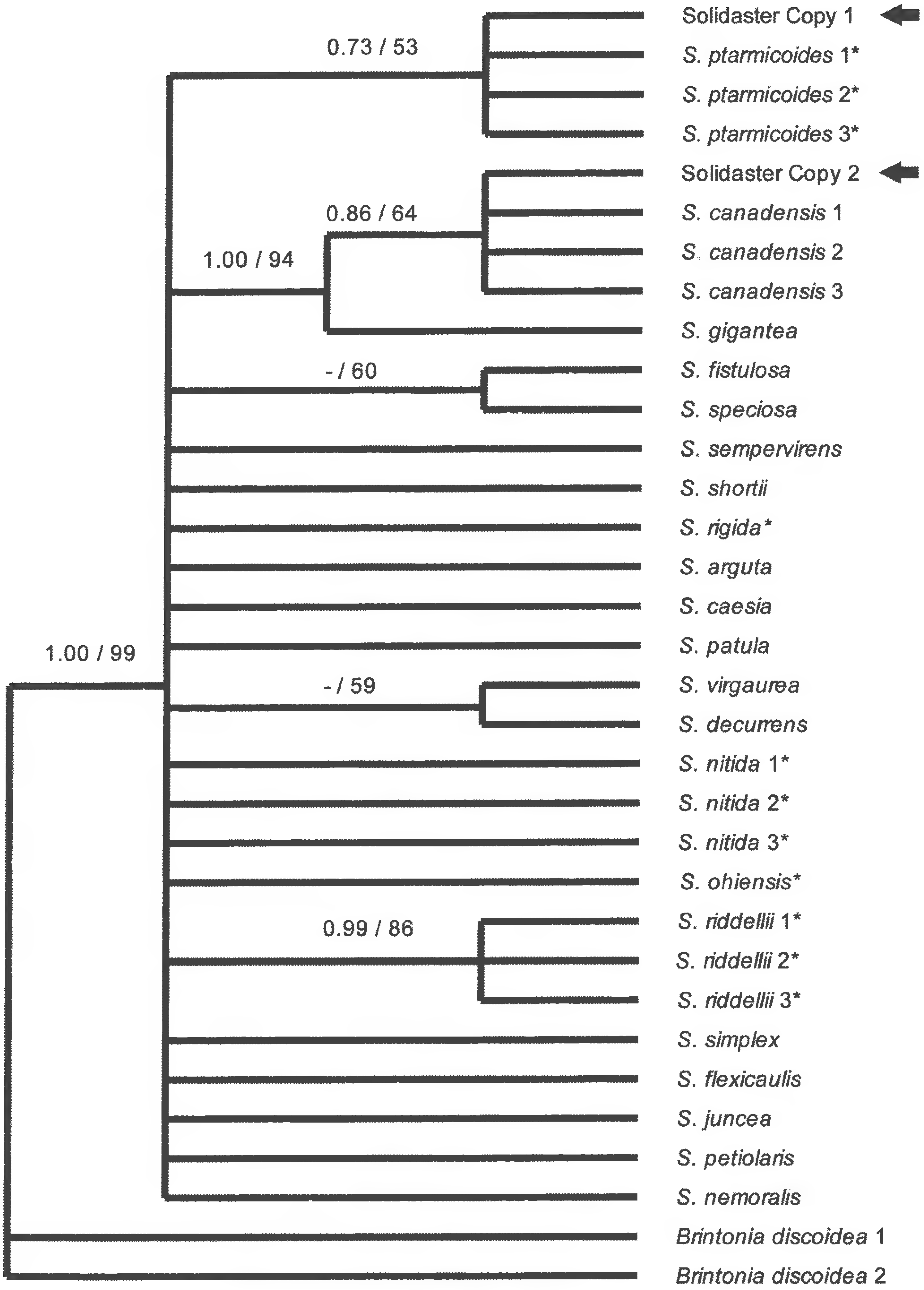

Fig. 3. Phylogenetic placement of ITS sequences from Solidaster cv. Lemore (arrows) relative to species of *Solidago* for which data were available. Shown is the strict consensus of 4576 minimum length trees in a single island (CI = 0.81 ; RI = 0.88) obtained from parsimony analysis, using *Brintonia* as outgroup. Support values from Bayesian and bootstrap (if greater than 50%) shown above branches. Asterisks designate species of *Solidago* sect. *Ptarmicoidea* (*Oligoneuron*).

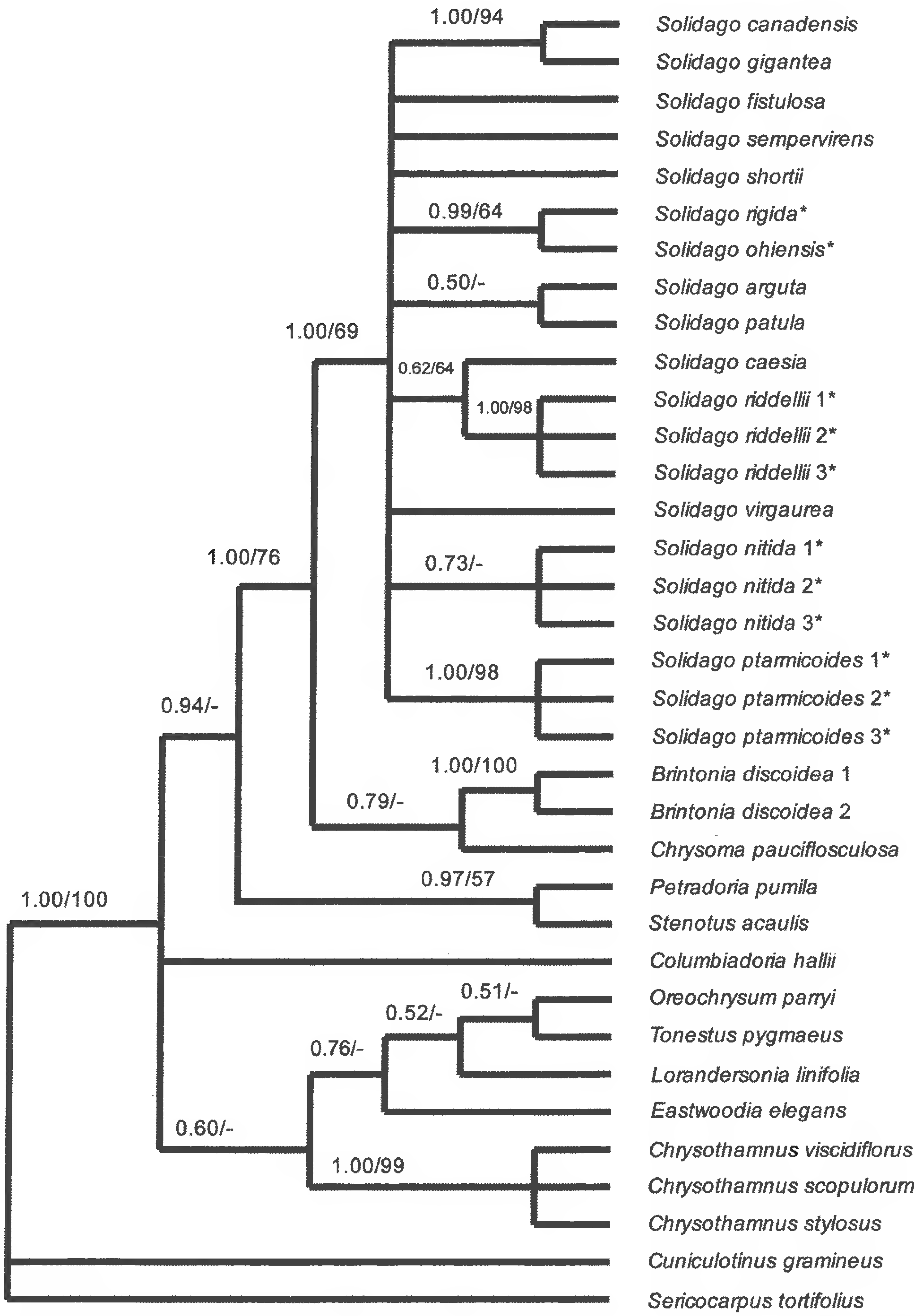

Fig. 4. Phylogenetic placement of *Solidago ptarmicoides* relative to *Solidago* and related genera, based on combined analysis of ITS and ETS data. Shown is the tree produced by Bayesian analysis (the strict consensus of 408 minimum length trees in a single island, CI=0.69, RI=0.85, obtained from parsimony analysis was topologically similar although with less resolution of clades), using *Cuniculotinus* and *Sericocarpus* as outgroups. Support values from Bayesian and bootstrap (if greater than 50%) shown above branches. Asterisks designate species of *Solidago* sect. *Ptarmicoidea* (*Oligoneuron*).

The major conclusion from phylogenetic analysis of ITS and ETS sequence data is that there is strong support for the inclusion of *S. ptarmicoides* within *Solidago*. Phylogenetic analysis clearly placed it in the clade corresponding to *Solidago* s.s (Fig. 4), and it differed in total sequence (ITS and ETS combined) from other members of *Solidago* by as little as a two bp differences (vs. *S. shortii*). There was also no support from sequence data to segregate *Oligoneuron*, represented in the data set by five of its six species including *S. ptarmicoides*, as a distinct genus; the combined ITS and ETS data in fact placed one of the *Oligoneuron* species, *S. riddellii*, with *S. caesia* from sect. *Solidago*, albeit with only weak support (Fig. 3, 4; see asterisks). The sequence data did, however, provide weak support for restricting the limits of *Solidago* to exclude *Brintonia* and *Chrysoma*, although the group formed by inclusion of these genera with *Solidago* would be monophyletic. These results largely mirror those presented by Zhang (1986; reproduced in Semple et al. 1999) based on chloroplast DNA restriction site data, and provide additional support for the most recent and comprehensive taxonomic treatment of the abovementioned taxa (Semple & Cook 2006).

A notable aspect of the ITS and ETS sequence data was the striking lack of divergence among members of *Solidago*. By contrast, ITS divergence in *Eupatorium* L. another genus of Asteraceae with a similar geographic range and occurrence in old field habitats, is 2–6% between species (12–43 bp differences; Schmidt & Schilling 2000; Schilling et al. 2007); *Eupatorium* is further differentiated from *Eutrochium* Raf., which are widely treated as congeners, by two indels (loss of a 13 bp region in *Eupatorium* and addition of a 3 bp region in *Eutrochium*) in addition to a minimum of 8% (33–61 bp) divergence. It should be noted that a previous chloroplast RFLP analysis (Zhang 1996) reports a higher level of variation within *Solidago*, and the resulting phylogeny strongly supports certain previously hypothesized groups. These contrasting levels of phylogenetic signal are best explained by the relative amount of DNA sequence scored in each study. Extrapolating from the values reported in Lane et al. (1996), approximately 2.5–3 kb of chloroplast sequence was assessed for variation in the Zhang study, compared to the approximately 1.1 kb ITS/ETS dataset analyzed here. In addition, previous work in Asteraceae indicates that chloroplast RFLP datasets can be more informative relative to those from ITS sequence (Morgan 1997). The most obvious possible source of the lack of ITS divergence in *Solidago* is that species level divergence is very recent. Other possible contributing factors include relatively large effective population sizes and the potential for homogenization through widespread interspecific hybridization followed by concerted evolution. Hybridization is traditionally viewed as widespread within *Solidago* (Cronquist 1980), and homogenization via concerted evolution is potentially a rapid process following hybridization (Franzke & Mummenhoff 1999). The relative lack of differentiation in ITS sequence between relatively distantly related congeners, which because of geographical considerations are unlikely to be part of a larger hybridization network, suggests that the primary cause is recency of divergence. This suggests that the striking ecological differences between *Solidago* species may have arisen during relatively short periods of time and indicates that resolving the phylogeny of *Solidago* will be a major challenge that will require markers evolving more rapidly than ITS and ETS.

APPENDIX

Collections of *Solidago* and related genera sampled for molecular analyses, with collector and herbarium or literature reference and GenBank numbers (ITS, ETS).

Solidago L. Solidaster cv. Lemore, *Schilling 07-06* (TENN), EU125353, EU125374. **Sect. Solidago, Subsect. Argutae,** *S. arguta* Aiton, *Beck 481* (MO), EU125354, EU125375; *S. patula* Muhl., *Beck 482* (MO), EU125355, EU125376. **Subsect. Glomeruliferae,** *S. caesia* L., *Beck 483* (MO), EU125356, EU125377; *S. flexicaulis* L., Kress et al. 2005, DQ005979. **Subsect. Humiles,** *S. simplex* Kunth, Kress et al. 2005, DQ005982. **Subsect. Juncea,** *S. juncea* Aiton, Kress et al. 2005, DQ005981. **Subsect. Maritimae,** *S. sempervirens* L., Urbatsch et al. 2003, AF477668, AF477732. **Subsect. Nemorales,** *S. nemoralis* Aiton, *Estes 1521* (TENN), EU125357. **Subsect. Solidago,** *S. virgaurea* L., *Dinies s.n.* (MO), EU125358, EU125378; *S. decurrens* Lour., GenBank Record, EF103140. **Subsect. Squarrosae,** *S. speciosa* Nutt., *Schilling* 07-05 (TENN), EU125359. **Subsect. Thyrsiflorae,** *S. petiolaris* Aiton, Noyes & Rieseberg 1999, AF046968. **Subsect. Triplinerve,** *S. canadensis* L., Urbatsch et al. 2003, AF477665, AF477729; *Laferriere 3564* (TENN), EU125360, –; *Weldon I 7/22/81* (TENN), EU125361; *S. gigantea* Aiton, *Beck 509* (MO), EU125362, EU125379; *S. shortii* Torr. & A. Gray, Beck et al. 2004, AY523854, [submit]. **Subsect. Venosae,** *S. fistulosa* Mill., Urbatsch et al. 2003, AF477666, AF477730. **Sect. Ptarmacoidei** (*Oligoneuron*), *S. ptarmicoides* (Torrey & A. Gray) B. Boivin, *Brandt 2603* (MO), EU125363, EU125380; *Dietrich 524*

(MO), EU125364, EU125381; *Anderson MO221*, EU125365, EU125382; *S. nitida* Torrey & A. Gray, *Thomas 141724* (MO), EU125366, EU125383; *Thomas 97470* (MO), EU125367, EU125384; *Thomas 138143*, EU125368, EU125385; *S. ohiensis* Riddell, *Kral 48497* (MO), EU125369, EU125386; *S. riddellii* Frank, *Smith 3617* (MO), EU125370, EU125387; *Vogt* 506 (MO), EU125371, EU125388; *Luges s.n.* (MO), EU125372, EU125389; *S. rigida* L., Beck et al. 2004, AY523851, EU125390. **Brintonia** Greene, *B. discoidea* (Elliott) Greene, Roberts & Urbatsch 2003, AY170930, AY169727; *Anderson 20021* (MO), EU125373, EU125391. **Chrysoma** Nutt., *C. pauciflosculosa* (Michx.) Greene, Urbatsch et al. 2003, AF477637, AF477701. **Chrysothamnus** Nutt., *C. scopulorum* (M.E. Jones) Urbatsch, R.P. Roberts & Neubig, Roberts & Urbatsch 2003, AY170956, AY169753; *C. stylosus* (Eastwood) Urbatsch, R.P. Roberts & Neubig, Roberts & Urbatsch 2003, AY170973, AY169770. *C. viscidiflorus* Nutt., Roberts & Urbatsch 2003, AY170947, AY169744. **Columbiadoria** G.L. Nesom, *C. hallii* (A. Gray) G.L. Nesom, Roberts & Urbatsch 2003, AY170948, AY169745. **Cuniculotinus** Urbatsch, R.P. Roberts & Neubig, *C. gramineus* (H. M. Hall) Urbatsch, R.P. Roberts & Neubig, Roberts & Urbatsch 2003, AY170936, AY169733. **Eastwoodia** Brandegee, *E. elegans* Brandegee, Roberts & Urbatsch 2003, AY170949, AY169746. **Lorandersonia** Urbatsch, R.P. Roberts & Neubig, *L. linifolia* (Greene) Urbatsch, R.P. Roberts & Neubig, Roberts & Urbatsch 2003, AY170936, AY169737. **Oreochrysum** Rydb., *O. parryi* Rydb., Roberts & Urbatsch 2003, AY170958, AY169755. **Petradoria** Greene, *P. pumila* Greene, Roberts & Urbatsch 2003, AY170959, AY169756. **Sericocarpus** Nees, *S. tortifolius* Nees, Urbatsch et al. 2003, AF477664, AF477728. **Stenotus** Nutt., *S. acaulis* Nutt., Roberts & Urbatsch 2003, AY170960, AY169757. **Tonestus** A. Nelson, *T. pygmaeus* A. Nelson, Roberts & Urbatsch 2003, AY170972, AY169769.

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NOVAE GESNERIACEAE NEOTROPICARUM XV: *KOHLERIA HYPERTRICHOSA*, A NEW SPECIES OF GESNERIACEAE FROM NORTHWESTERN ECUADOR

John Littner Clark

Department of Biological Sciences
Box 870345
The University of Alabama
Tuscaloosa, Alabama 35487-0345. U.S.A.
jlc@ua.edu

Laurence E. Skog

Botany Department, MRC-166
Smithsonian Institution, PO Box 37012
National Museum of Natural History
Washington, DC 20013-7012. U.S.A.
skogl@si.edu

ABSTRACT

A new species of *Kohleria* (Gesneriaceae, tribe Gloxinieae) is described from the Andean cloud forests of the Carchi and Esmeraldas provinces in northwestern Ecuador where it is an abundant local endemic. The remarkable long wooly trichomes in combination with a fruit dehiscing by a single dorsal slit and epiphytic habit differentiate **Kohleria hypertrichosa** from other species of *Kohleria*.

RESUMEN

Se describe una nueva especie de *Kohleria* (Gesneriaceae, tribe Gloxinieae) de los bosques nublados andinos de las provincias de Carchi y Esmeraldas en el noroeste de Ecuador, en donde es una especie endémica abundante localmente. Los largos tricomas lanosos junto con la dehiscencia del fruto por medio de una hendidura dorsal y el hábito epifítico diferencian a **Kohleria hypertrichosa** de otras especies de *Kohleria*.

Key Words: *Kohleria, Capanea, Monopyle*, Ecuador, Gesneriaceae

The most recent treatment of the genus *Kohleria* Regel is that by Kvist and Skog (1992), who recognized 17 species. More recently, Roalson et al. (2005a) transferred the two species of the genus *Capanea* Decaisne ex Planchon to *Kohleria* making it currently a genus of 19 recognized species. The revised circumscription of *Kohleria* to include *Capanea* (Roalson et al. 2005a) is based primarily on molecular data from the nuclear ribosomal DNA internal transcribed spacer region, the chloroplast DNA *trnL* intron and *trnL-trnF* intergenic spacer region (Roalson et al. 2005b). Traditional *Kohleria* (e.g., the recent monograph by Kvist and Skog, 1992) would be paraphyletic with the exclusion of *Capanea*. Thus, many of the features that differentiated *Capanea* are autapomorphic for a well-supported clade nesting in *Kohleria* (Roalson et al. 2005b).

The new species described here has a history of being collected in the Carchi province where it is locally abundant in cloud forests. It was initially assumed to be a new species of *Capanea* by Hans Wiehler when it was collected and appeared in a photograph in the horticultural journal *The Gloxinian* (McDowell 1995). Images of *K. hypertrichosa* also appeared in the *Gesneriad Journal* as a new species of *Capanea* in a report of a collecting expedition to Ecuador (Dunn 1997). The species was assumed to be a member of this formerly recognized genus because of the woolly pubescence, the shape of the corolla, and its epiphytic habit. Vegetatively *Kohleria hypertrichosa* appears similar to *Monopyle* because of the strongly anisophyllous leaves and dorsiventral shoots. In the type locality of *Kohleria hypertrichosa*, the species *Monopyle macrocarpa* Benth. is also abundant (cf., field collection *J.L. Clark 6298*). The two species often grow side-by-side and telling them apart vegetatively is challenging.

The species described here is remarkable in that it has been collected and specimens annotated as belonging to *Monopyle* or *Capanea*, but not *Kohleria*. The correct placement of this new species has perplexed many Gesneriaceae workers because of its habit (facultative epiphyte instead of the more typical terrestrial habit in *Kohleria*); thick wooly pubescence on the outer surface of the corolla (more typical of *Capanea*); and strongly anisophyllous leaves (more typical of *Monopyle*). The key synapomorphy for recognizing traditional *Kohleria* is a fruit dehiscing by a single dorsal slit from apex to base (Figs. 1D and 2G). The presence of this type of fruit in this species was unknown until it was observed and photographed in 2001 (cf., field collection *J.L. Clark 6288*). Many other collectors (e.g., Tirado and Hoover) had documented this new species in

flower, but not in fruit, thus making it a difficult species to place without molecular data. The presence of a bilobed stigma is a notable feature that *K. hypertrichosa* shares with most congeners. A stomatomorphic stigma is present in *Monopyle* and is an autapomorphy in the two traditionally recognized species of *Capanea* that were recently combined in *Kohleria* (Roalson et al. 2005a).

Another morphological feature of many species in *Kohleria*, which is also present in *K. hypertrichosa*, is the presence of a ventricose apical pouch on the lower side of the corolla. The ventricose pouch in *K. hypertrichosa* is sometimes obscured after anthesis and on pressed herbarium collections (e.g., the pouch was not apparent in early photographs and collections such as *J.L. Clark & R.W. Dunn 2406* and *J.L. Clark et al. 2408*).

The generic placement of *K. hypertrichosa* is also strongly supported by molecular data from the nuclear ribosomal DNA internal transcribed spacer region, the chloroplast DNA *trnL* intron and *trnL-trnF* intergenic spacer region (Roalson et al. 2005b). One of the samples that appeared in the phylogeny published by Roalson et al. is a tissue sample from silica gel-dried leaves of a paratype of *K. hypertrichosa* (cf., field collection *J.L. Clark & R.W. Dunn 2446*). The specific collection is noted in Roalson et al. (2005b) as, "*Kohleria* sp. nov. 2446" where it was shown as being strongly supported as the sister taxon to *Kohleria villosa* (Fritsch) Wiehler.

Kohleria hypertrichosa J.L. Clark & L.E. Skog, sp. nov. (**Figs. 1–2**). Type: ECUADOR. Carchi: Cantón Espejo, Parroquia Guatal, Mirador de las Golondrinas (Fundación Golondrinas), trail from Santa Rosa (El Rosal) to the refugio at El Corazon, 00°49'46"N, 78°07'03"W, 1600–2000 m, 5 Jul 2003, *J L. Clark, S.G. Clark, E. Folleco & B. Syka 8450* (holotype: US; isotypes: AAU, BRIT, C, CAS, COL, E, F, GH, K, MO, NY, QCA, QCNE, SEL, UNA, US, W).

A speciebus congeneribus omnino in tres characteribus combinatis: in habitis epiphyticis pro parte maxima et in corollis perlanatis et in fructis bivalvatis sed dorsaliter longitudinaliter unifissis, distincta.

Facultative epiphytic climber; rarely terrestrial, stems dorsiventral to erect, frequently branched, to 2 m long, subwoody to herbaceous, terete, glabrescent below, densely pilose to sericeous above. *Leaves* opposite, unequal in a pair; larger leaf with petioles terete, 3–10 mm long, green, densely sericeous, blade subcoriaceous when dry, elliptic to slightly falcate, 6–14 × 1.5–4 cm, base acute and occasionally asymmetrical, apex attenuate, margin serrate, adaxially pale green, sparingly to densely pilose (especially on veins), abaxially green to reddish-green, uniformly pilose; smaller leaf with petioles sessile to 3 mm long, green, densely sericeous, blade subcoriaceous when dry, broadly ovate (rarely narrowly ovate), 1–2.5 × 1–1.5 cm, base and apex rounded, margin serrate, adaxially pale green, sparingly to densely pilose (especially on veins), abaxially green to reddish-green, uniformly pilose. *Inflorescence* epedunculate, reduced cyme, appearing fasciculate, with 1 (rarely 2) flower per node at or near stem apices; bracteoles absent; pedicels longer than the petiole, 1.5–3 cm long, densely sericeous. *Flowers* zygomorphic, not resupinate; calyx lobes 5, ventral lobe free, lateral and dorsal lobes basally connate for 3–5 mm, lobes erect at anthesis, reflexed in fruit, equal, ovate, 1.5–2.0 × 0.5–1.0 cm, apex acute, margin nearly entire with 1–3 pairs of serrations, bright red, outside densely sericeous, inside sparsely sericeous; corolla horizontal in calyx; 2.5–3.0 cm long; base 1 cm in diameter, middle ampliate, becoming apically ventricose on lower surface, throat slightly constricted, appearing laterally compressed, to 1 cm wide (at mouth), outside yellowish-white, covered with dense villous white pubescence, inside mostly yellow with red spots, mouth with glandular trichomes, lobes glabrous, red, subequal, rotund, to 3 mm long, to 5 mm wide, rounded, entire; nectary of five separate glands evenly distributed around ovary, each 1.0–1.5 mm high and 0.5–1.5 mm wide at base, glabrous; stamens 4, didynamous, included; filaments 1.6 cm long, adnate to the base of the corolla tube, pilose; anthers longer than broad, ca. 2 mm long, ca. 1.5 mm wide, dehiscing by longitudinal slits; staminode not observed; ovary inferior, villous, 2–5 × 3–6 mm, style 9–12 mm long, sericeous, stigma included, forked. *Fruit* an oblong capsule, 20–30 mm long, diameter 4–8 mm, dehiscing by a single dorsal slit from apex to base; seeds numerous, subglobose, irregularly striate, 0.4 × 0.3 mm, dark brown.

Phenology.—Flowering in January, April, May, November, and December. The only collections with fruits are from May, July, and December.

Distribution.—*Kohleria hypertrichosa* is known from northwestern Ecuadorian cloud forests on the western Andean slopes of the Carchi and Esmeraldas provinces from 1100 to 2000 meters. It is locally

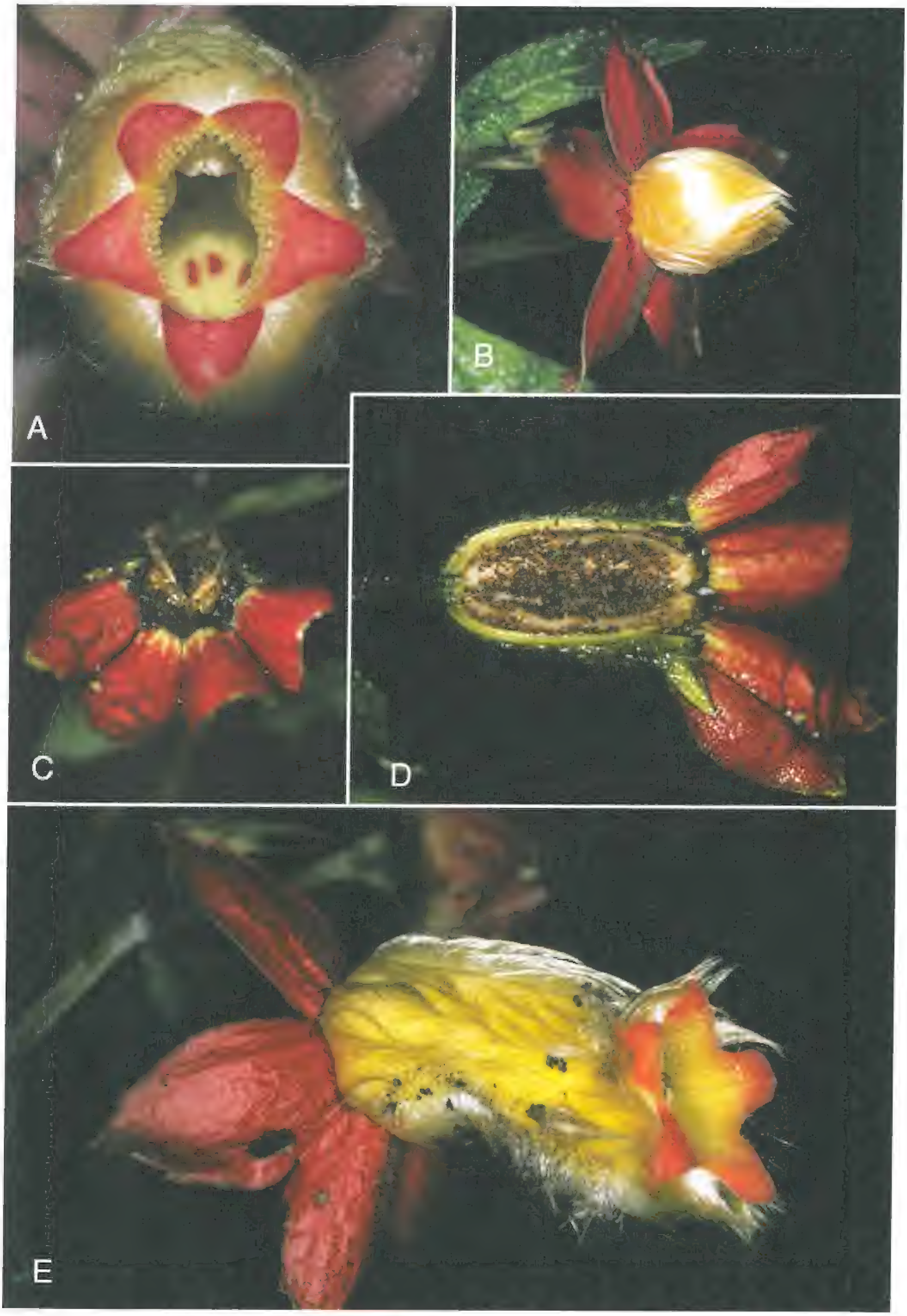

Fig. 1. *Kohleria hypertrichosa* J.L. Clark & L.E. Skog. A. Front view of corolla. B. Immature flower. C. Front view of capsule. D. Fruit dehiscing by a single dorsal slit. E. Lateral view of flower. (A from *J.L. Clark et al. 6359*; B & E from *J.L. Clark et al. 8462*; C & D from the holotype, *J.L. Clark et al. 8450*)

Fig. 2. *Kohleria hypertrichosa* J.L. Clark & L.E. Skog **A.** Habit. **B.** Side view of flower. **C.** Face view of flower. **D.** Glandular trichomes on mouth of corolla. **E.** Corolla opened to show stamens. **F.** Calyx opened and corolla removed to show valvate nectary glands. **G.** Mature fruit. **H.** Seeds. (A–H from *J.L. Clark et al. 6359*).

abundant sometimes covering trees and trailsides, especially in the Mirador de las Golondrinas, a private reserve managed by Fundación Golondrinas and the Gualpi area near the Reserva Awá (collections exist both inside and outside the Territorio Awá). No collections of *Kohleria hypertrichosa* have been made outside of the Carchi and Esmeraldas provinces, but it is likely to also occur in the adjacent Department of Nariño, Colombia where limited recent botanical exploration has taken place.

Etymology.—The epithet *hypertrichosa* is derived from the congenital condition of generalized "Hypertrichosis," the medical term referring to a condition of excessive growth of body hair in humans. The condition is commonly known as "Werewolf syndrome" which comes from a mythological werewolf of which the person is completely covered in hair or fur. Although not commonly grown in cultivation, the plant species is known among horticulturalists as "Chewbacca," for the famous hairy biped character ("Wookie") from the popular cult phenomenon 1977 movie Star Wars IV: A New Hope.

Paratypes. **ECUADOR. Carchi:** Cantón Espejo, Bosque Protector Mirador de Golondrinas, between the village Las Juntas and la Cabaña del Corazón, 00°49'N, 78°01'W, 1360–2000 m, 8 Apr 1996, *J.L. Clark, P. Sabbe & R.W. Dunn 2408* (MO, QCNE, SRP, US); Cantón Espejo, Bosque Protector Mirador de Golondrinas, trail SW of La Cabaña del Corazón that passes the latrine, 00°49'N, 78°01'W, 2000 m, 9 Apr 1996, *J.L. Clark & R.W. Dunn 2446* (MO, QCNE, SRP, US); Cantón Espejo, Bosque Protector Mirador de Golondrinas, between the village of Las Juntas and La Cabaña del Corazón, 00°49'N, 78°01'W, 1400–2000 m, 10 Apr 1996, *J.L. Clark & R.W. Dunn 2466* (MO, QCNE, SRP, US); Cantón Tulcan, Parroquia Chical, path from the village of Quinyal towards an area known locally as "Gualpi" (near the border of the Reserva Awá), 00°57'54"N, 78°21'W, 1200–1700 m, 6 Dec 2001 (fr), *J.L. Clark & O. Mejia 6288* (MO, QCNE, US); Cantón Tulcan, Parroquia Chical, path from the village of Chical towards an area known locally as "Crystal" via Río Blanca and the Cordillera Gualchan (ca. 6–8 km SW of Chical), 00°53'49"N, 78°34'W, 1200–1800 m, 7 Dec 2001 (fl, fr), *J.L. Clark, O. Mejia & E. Diaz 6359* (CAS, E, F, K, MO, NY, QCA, QCNE, US); Cantón Espejo, Parroquia Guatal, Mirador de las Golondrinas (Fundación Golondrinas), trail from El Corazon towards La Cortadera (2 km NE of refugio), 00°49'46"N, 78°07'03"W, 2000–2500 m, 6 Jul 2003 (fr, fl), *J. L. Clark & E. Folleco 8462* (AAU, CAS, COL, E, F, K, MO, NY, QCNE, SEL, US, UNA); forest along trail from Rafael Quindi's house to his mountain finca, 00°52'N, 78°8'W, 1890 m, 28 Nov 1987 (fl), *W.S. Hoover & S. Wormley 1906* (MO); embankments along Río Verde, from point at which trail from Rafael's Mountain Finca crosses river, 1.5 km, 00°52'N, 78°8'W, 1890 m, 29 Nov 1987 (fl), *W.S. Hoover 1918* (MO); ridge to NE of Rafael Quind's mountain finca, 0°52'N, 78°8'W, 2000 m, 29 Nov 1987 (fl), *W.S. Hoover 2046* (MO); Gualpi Chico, Awá encampment, trail on reservation border going north, 00°58'N, 78°16'W, 1330 m, 15 Jan 1988 (fl), *W.S. Hoover, P. Gelpi, R.A. Lorentzen & A. Arguello 2463* (MO, US); near encampment in Gualpi Chico area of Awá Reserve, 00°58'N, 78°16'W, 1330 m, 20 Jan 1988 (fl), *W.S. Hoover, A. Arguello, P. Gelpi & R.A. Lorentzen 2832* (MO, US); trail to Pailon on encampment, Gualpi Chico area of Awá, 00°58'N, 78°16'W, 1350–1400 m, 21 Jan 1988 (fl), *W.S. Hoover, A. Arguello, P. Gelpi & R.A. Lorentzen 3618* (MO, US); Cantón Tulcan, Parroquia Tobar Donoso, sector El Baboso, Reserva Indígena Awá, 00°53'N, 78°20'W, 1600 m, 3 Oct 1991 (fl), *G. Tipaz, D. Rubio & M. Taicuz 267* (SEL, US); Cantón Espejo, Parroquia Tobar Donoso, Reserva Indígena Awá, centro Baboso, 00°53'N, 78°25'W, 1800 m, 17–27 Aug 1992 (fl), *G. Tipaz, M. Tirado, C. Aulestia, N. Gale & P. Ortiz 1800* (US); Cantón Mira, El Carmen, Cerro Golondrinas, 00°50'N, 78°11'W, 2000–2400 m, 18–25 Aug 1994 (fl), *M. Tirado, P. Fuentes, R. Zurita & L. Chamorro 1286* (MO, QCNE, US); Espejo, Reserva Golondrinas, El Corazón, sendero a Río El Corazón, 00°50'N, 78°08'W, 2010 m, 24 Jan 2004 (fl), *H. Vargas et al. 4406* (MO, US); **Esmeraldas:** Cantón San Lorenzo, Parroquia Alto Tambo, mature forest 4–8 km W of El Cristal, 00°50'16"N 078°31'04"W, 1500–1650 m, 27 May 2008 (fr), *J.L. Clark, J. Melton III & O. Solarte 10310* (CAS, E, F, K, MO, NY, QCNE, SEL, UNA, US, W); Cantón San Lorenzo, Parroquia Alto Tambo, mature forest 4–8 km W of El Cristal, 00°50'16"N 078°31'04"W, 1500–1650 m, 27 May 2008 (fl), *J.L. Clark, J. Melton III & O. Solarte 10311* (QCNE, SEL, UNA, US); area of Cristal, above Lita, 1100–1150 m, 24 Apr 1995 (fl), *H. Wiehler et al. 9574* (SEL, US).

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TWO NEW SPECIES OF *GUADUA* (BAMBUSOIDEAE: GUADUINAE) FROM COLOMBIA AND BOLIVIA

Ximena Londoño

Instituto Vallecaucano de Investigaciones Cientificas
AA 11574, Cali, COLOMBIA
ximelon@telesat.com.co

Eneida Zurita

Herbario Nacional Forestal "Martin Cárdenas"
Cochabamba, BOLIVIA
eneidaz@gmail.com

ABSTRACT

Guadua incana and **G. chaparensis,** two new species of woody bamboo from South America, are described and illustrated. **Guadua incana,** from southeastern Colombia, has been found in the foothills of the eastern side of the Cordillera de los Andes, and **G. chaparensis,** from Bolivia, occurs in the Amazon lowlands in the District of Chapare. Based on morphological evidence, **G. incana** and **G. chaparensis** are closely related to **Guadua weberbaueri,** which is lectotypified here. We discuss other related species and provide a key to them.

RESUMEN

Se describen e ilustran dos especies nuevas para Sur América, **Guadua incana** y **G. chaparensis. Guadua incana** del suroriente de Colombia, crece en el pie de monte de la vertiente oriental de la Cordillera de los Andes, y **G. chaparensis** de Bolivia, se localiza en el Distrito Biogeográfico Amazónico del Chapare. Con base en evidencias morfológicas, **G. incana** y **G. chaparensis** se relacionan entre si y también con **Guadua weberbaueri,** la cual se lectotipifica aquí. Además, se hacen comentarios sobre otras especies afines y se incluye clave para identificación.

During a 1987 field trip to Caquetá and Putumayo, Colombia (Colciencias-Inciva Project No. 2108-07-009-85), sterile specimens of a new species of *Guadua (Londoño & Quintero 144 & 214)* were collected. A living rhizome was brought to the bamboo germplasm bank of the Juan Maria Cespedes Botanical Garden in Tuluá, Valle del Cauca, Colombia, and after 14 years in cultivation (1987–2001), accessions *Londoño 144 & 214* flowered and made possible their identification.

Because of the absence of flowering material in the majority of woody bamboo herbarium specimens (in part, a result of their long flowering cycles), several species of bamboo are described from vegetative material alone, e.g., *Eremocaulon setosum* Londoño & L.G. Clark, *Chusquea riosaltensis* L.G. Clark and *Ch. caparaoensis* L.G. Clark (Londoño & Clark 2002a; Clark 1992). Vegetative characters such as culm leaves, buds, branches and rhizomes have been utilized to delimit many new species (McClure 1966; Judziewicz et al. 1999; Soderstrom & Young 1983). We waited 14 years for the opportunity to describe *G. incana* with flowering material, but for the new species from Bolivia, *G. chaparensis* Londoño & Zurita, we decided to describe it on the basis of sterile material alone, in order to provide a name for this distinctive species.

In addition to the vegetative and reproductive characters used to delimit *G. incana*, the genetic AFLP analysis done by Marulanda et al. (2002) reported a clear genetic differentiation between *G. incana* and *G. angustifolia* (accessions, varieties and biotypes), and also between *G. incana* and *Guadua uncinata* Londoño & L.G. Clark (2002b), a species that is sympatric with *G. incana*. This genetic result helped corroborate the diagnostic morphological features that identify *Guadua incana* as a new species.

Guadua chaparensis was collected by the second author in central Bolivia. It occurs not only in the type locality (Comunidad Israel) but in various communities such as Capinota, Hermanos Ledesma, Agua Rica, 24 de Septiembre, Monte Sinaí, Villa Jerusalen, Villa Imperial, Valle de Sajta, Valle Ivirza, Villa Nueva, Alto San Pablo, Tarija and Puerto Aroma, all of them in the Chapare area.

The two new species, *G. incana* and *G. chaparensis*, are clearly referable to *Guadua* based on their long-necked rhizomes, white bands on the culms, thorny branches, triangular culm leaves, and, in the case of *G. incana*, pseudospikelet structure with winged-keeled palea (Judziewicz et al. 1999). Both species are closely related,

grow in lowland tropical rain forests, and appear to be endemic to the localities in which they were collected. Both are also utilized by local communities for corrals, fences, water conduction and light rural construction.

Guadua weberbaueri, the taxon most closely allied to the two new species, was described by Pilger (1905), who selected as the holotype number 4562 collected by the German botanist August Weberbauer (1871–1948) in Moyobamba, Perú. As with many other collections by Weberbauer, the type chosen by Pilger and deposited in Berlin (B) was destroyed during World War II. In 1991, the first author visited the herbarium of the Universidad Nacional Agraria, La Molina (MOL) in Lima, Peru, and found a complete duplicate of *Weberbauer 4562*. This isotype, which we have selected to serve as the lectotype, includes a foliage leaf complement and one inflorescence branch.

Morphological study reveals that *Guadua weberbaueri* Pilger, *G. tagoara* (Nees) Kunth and *G. sarcocarpa* Londoño & Peterson (1991) share several features with each other and the two undescribed species, forming the basis for a group within *Guadua*, here recognized informally as the *G. weberbaueri* Group (Table1). The following combination of characters delimits this group: a) culms erect at the base with the apical portion leaning on or pendent from trees; b) internodes hollow, with walls up to 1.5 cm thick, elongated up to 90 cm; c) culm leaves with persistent blades, these 1/4 to 1/5 as long as the sheaths; d) culm leaves with canescent inner ligules; e) synflorescences terminating in leafy or leafless branches with capitate coflorescences in the earliest state of development; f) pseudospikelets with wide-winged palea keels (0.8 to 2.5 mm); and g) ovaries fusoid in shape.

These five species, *Guadua weberbaueri*, *G. sarcocarpa*, *G. incana*, *G. chaparensis* and *G. tagoara*, grow in very humid, lowland forests and they have in common the presence of water inside of the hollow internodes. Herbarium labels from *Guadua sarcocarpa* (*Calderon & Soderstrom 2348*-US#2810196 and *Smith 5275*-US#3080541), the description for *G. tagoara* in Londoño and Clark (2002b), and Louton et al. (1996) for *G. weberbaueri* reported the presence of internodes filled with water. This internal water phenomenon seems to be associated with very high relative humidity and a high water table. Why water accumulates inside the internodes is still uncertain. It may occur after strong changes of temperature that break tissues allowing water to leak into and accumulate in the lumen.

A key to the species of the *G. weberbaueri* group based on vegetative characters is presented here.

KEY TO SPECIES OF THE *GUADUA WEBERBAUERI* GROUP

1. Culm leaves abaxially puberulous to pubescent, the indument detached only with difficulty from the surfaces, the margins slightly discontinuous at the junction of the sheath and blade.
    2. Foliage leaf sheaths abaxially pubescent, bearing fimbriae at the summit; folage leaf blades abaxially pilose and inconspicuously tessellate; inner ligules pubescent; pseudopetioles abaxially setose-pilose; culm leaf auricles absent ____ **G. weberbaueri**
    2. Foliage leaf sheaths abaxially glabrous with oral setae and fimbriae at the summit; foliage leaf blades abaxially irregularly glabrescent and conspicuously tessellate; inner ligules glabrous; pseudopetioles abaxially glabrous; culm leaf auricles absent or present ____ **G. sarcocarpa**
1. Culm leaves abaxially densely pubescent to canescent, the indument easily detached from the surfaces, the margins continuous or slightly discontinuous at the junction of the sheath and blade.
    3. Culms erect below with spreading branches above, and leaning on or pendent from trees; foliage leaf blades glabrous on bot surfaces and abaxially strongly tessellate; pseudopetiole abaxially glabrous; Brazil ____ **G. tagoara**
    3. Culms erect below, arching apically, lacking spreading branches above and not leaning on or pendent from trees.
        4. Foliage leaf sheaths glabrous, fimbriae at the summit, fimbriae 4–5 mm long; inner ligules glabrous; leaf blades abaxially subglabrous; pseudopetioles abaxially glabrous; Colombia ____ **G. incana**
        4. Foliage leaf sheaths subglabrous, not fimbriate at summit; inner ligules puberulous; leaf blades abaxially glabrous; pseudopetioles abaxially glabrescent; Bolivia ____ **G. chaparensis**

Guadua incana Londoño, sp. nov. (**Fig. 1**). TYPE: COLOMBIA. CAQUETÁ: Km 26.7 via Florencia-Guadalupe, Quebrada La Rebolcosa, vertiente oriental de la Cordillera Oriental, 750 m, cultivated at the Botanical Garden Juan María Céspedes, 2 Jun 2001 (fl), *X. Londoño 972* (HOLOTYPE: COL!, ISOTYPES: CUVC, TULV, ISC, US).

Bambusa lignosa, spinosa. Rhizoma sympodiale, pachymorphum. Culmi 10–15(–18) m alti, 7–9(–12) cm diam.; internodia (20–)30–65 cm longa, cava. Folia culmorum leviter coriacea, canescentia, deciduas, vagina et lamina conspicue distinctae in ju-

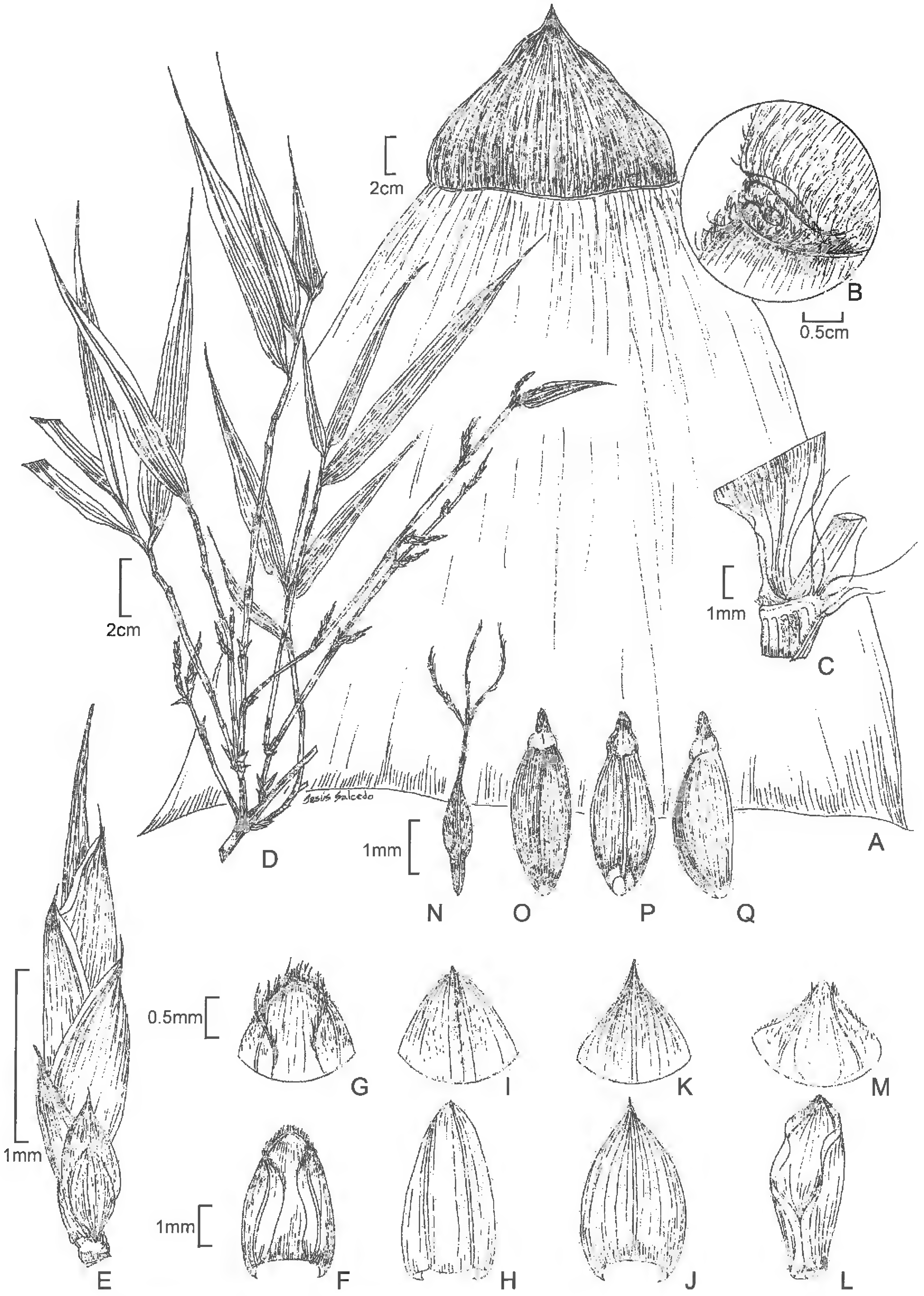

Fig. 1. *Guadua incana*. A. Culm leaf, adaxial view. B. Detail of culm leaf showing blade base and sheath summit, adaxial surface. C. Foliage leaf ligular area, abaxial view. D. Mid-culm node with branch complement of leafy flowering axis. E. Pseudospikelet showing basal gemmiparous bracts, a sterile lemma, fertile florets, and terminal rudimentary florets. F–G. Prophyll, abaxial view and apex. H–I. Basal gemmiparous bracts, abaxial view and apex. J–K. Lemma, abaxial view and apex. L–M. Palea, abaxial view and apex. N. Gynoecium with three stigmas. O–Q. Caryopsis with a stylar column; dorsal view showing the hilum (O), frontal view showing the embrotegium (P), and lateral view (Q). (A–C, *Londoño 144*, TULV; D–Q, *Londoño 972* TULV).

ventute; vagina (19–)24–33 cm longa; lamina (3.5–)5–10 cm longa, persistens, erecta, triangularis. Ramificatio intravaginalis. Folia ramorum cujusquisque complementi 5–8(–10); vagina subglabra, fimbriata, margine imbricata, conspicue ciliata; pseudopetiolus 2–4 mm longus; lamina (3.5–)11–13(–16) cm longa, (0.7–)1–2(–2.2) cm lata, lineari-lanceolata. Synflorescentia 1–4(–6) coflorescentiis, 1–5 multifloris pseudospiculis munitis. Pseudospiculae 2–4 cm longae, 0.4–0.7 mm lata; lemma 9–11.5 mm longum, 6–8 mm latum; palea 9–11 mm longa, 4–5 mm lata. Ovarium fusiforme, (1.5–)2–3 mm longum, 0.4–0.5 mm latum.

Woody, thorny bamboo. Rhizomes pachymorph. **Culms** 10–15(–18) m tall, 7–9(–12) cm in diam., erect at base, arching apically, whitish-green when young; **internodes** (20–)30–55(–65) cm long, cylindrical, hollow, some filled with water, the wall 1–1.5 cm thick, the surface whitish-green pubescent when young, becoming evidently whiter below the nodal line, covered by very appressed, white, soft, slender, retrorse hairs; **nodes** solitary, the nodal line horizontal, with a supranodal band 1–1.7 cm wide of appressed, white, soft, slender hairs, and an infranodal band 1.5–2 cm wide of long, soft, slender, white, appressed hairs, the two bands unambiguously evident, the supranodal ridge slightly pronounced, the canescence from the infranodal band extending 2/3 along the internode; **bud** single, triangular, the shoulders of the prophyll ciliate. **Culm leaves** (22–)30–44 cm long, 29–44 cm wide at the base, coriaceous, deciduous, triangular, blade and sheath conspicuously distinguished by color and pubescence when young; **sheaths** (19–)24–33 × 29–44 cm, whitish-green with yellowish spots when young, becoming whitish-brown to stramineous, abaxially canescent-hispid, densely covered by two different types of hairs (1) short, matted, white and wavy hairs, looking like wool and easily detached, and (2) straight, stiff, sharp, amber hairs, up to 3 mm long, adaxially glabrous and shiny, the margins papery, the overlapping one ciliate, the cilia transparent, up to 2.5 mm long; **inner ligules** 0.5–1.0 mm long, truncate, straight to slightly curled in the middle, extending completely from margin to margin, adaxially glabrous, abaxially canescent, densely ciliate on the margin, the cilia up to 0.6 mm long, whitish in color and conspicuous; **blades** (3.5–)5–10 × 7–12 cm, 1/4–1/5 as long as the sheath, triangular, erect, persistent, inflated, green to reddish-green when young then brown, abaxially glabrous at the central inflated part, sparsely hispid and pubescent through the apex and marginally, adaxially densely pubescent between the nerves, covered by two types of hairs (1) firm, stiff, transparent hairs up to 2.5 mm long, and (2) short, soft, loose hairs up to 0.5 mm long, the margins papery, shiny and smooth at the middle and upper portion, basally ciliate, wrinkled at the junction with the sheath and bearing conspicuous fimbriae and cilia, the cilia up to 2.5 mm long, hyaline, rubbing off at the middle and upper portion, the fimbriae 3–5 mm long, ivory, wavy to curled, basally scabrid, apically smooth, the apex strongly mucronate and usually split in two parts, the mucro up to 1 mm long. **Branching** intravaginal, consisting of one main branch and 1 to 2 secondary branches, the branches manifestly armed, thorns 1 to 3(–4) per node, the central one dominant, bigger and straight to slightly curved, the other two slightly curved to curved. **Foliage leaves** 5 to 8(–10) per complement; **sheaths** abaxially pubescent to glabrous, usually with a patch of villous hairs on one side of the midnerve at the upper portion, green when young then stramineous, the overlapping margin conspicuously ciliate, the underlapping one minutely cililate to smooth and papery, bearing a few fimbriae at the summit; fimbriae 4–5 mm long, ivory, basally straight and scabrid, apically wavy to curled and smooth; **inner ligules** 0.2–0.3 mm long, short, brown, puberulous, ciliolate to smooth at the margin; **outer ligules** 0.3–0.4 mm long, stramineous, glabrous, shiny, the margin ciliolate to smooth; **pseudopetioles** 2–4 mm long, adaxially scabrous toward one margin, otherwise glabrous, abaxially glabrous, pulvinate, the pulvinous villous, stramineous to brown; **blades** (3.5–)11–13(–16) × (0.7–)1–2(–2.2) cm, L:W = 5–14:1, 13–15 nerved, linear-lanceolate, adaxially glabrous to subglabrous, with scattered, strigose, transparent hairs up to 1.2 mm long, with 4–6 raised scabrid submarginal nerves on one side, becoming basally evidently scabrous by one side, abaxially glabrous to subglabrous, with scattered strigose, transparent hairs up to 1 mm long, papillose and tessellate, the midnerve and primary nerves prominent and yellow in the middle and lower portion, one margin scabrid, the other scabridulous, the apex acuminate, with a mucro 2–3 mm long. **Synflorescences** terminating usually leafy branches of all orders, polytelic, consisting of 1–4(–6) coflorescences with 1–3(–5) multiflowered pseudospikelets; **main axes** basally glabrous, apically pilose; **subtending bracts** varying in size and shape through the main axis, from fully developed and similar to a small foliage leaf to triangular with a reduced apiculus, the blades

Table 1. Comparison of vegetative morphological characters of *Guadua incana, G. chaparensis, G. tagoara, G. weberbaueri,* and *G. sarcocarpa.*

CHARACTER	*incana*	*chaparensis*	*tagoara*	*weberbaueri*	*sarcocarpa*
Culm habit	erect basally, arching apically	erect basally, arching apically	erect basally, branching and reaching over trees	erect basally, arching apically	erect basally, branching and reaching over trees
Culm size					
length (m)	10–15(–18)	18–25	10–15(–20)	8–15(–20)	10–20(–30)
diameter (cm)	7–9(–12)	(3.5-)7–12	5–10	4–8(–12)	8–10
Internode size					
length (cm)	20–65	22–70	25–80	25–70	25–90
wall thickness (cm)	1–1.5	1–1.5	0.5–1	1–1.5	1
Culm leaf auricles	absent	absent	absent	absent	absent/present
Culm leaf inner ligule					
size (mm)	0.5–1	0.5–1	1–2	1–3	2–3
abaxial indument	canescent	canescent	canescent	canescent	canescent
Foliage leaf sheath					
indument	subglabrous, with a patch of hairs at the apex	subglabrous with a patch of hairs at the apex	subglabrous with a patch of hairs at the apex	subglabrous	glabrous
margin	conspicuously ciliate	conspicuously ciliate	ciliate	ciliate	smooth and papery
summit	fimbriate	glabrous	fimbriate, rarely with auricles	fimbriate	oral setae or fimbriae
Pseudopetiole					
length (mm)	2–4	2–4	4–10(–15)	5–7	(4–)6–10
abaxial indument	glabrous	glabrous	glabrous	setose-pilose	glabrous
Foliage leaf blade, abaxial indument	glabrous to subglabrous	glabrous	glabrous	pilose to glabrous	irregularly subglabrous
Pseudospikelet size (cm)	2–4 x 0.4–0.7	not seen	0.5–4 x 0.2–0.6	0.5–2.5 x 0.2–0.7	1.2–8.5 x (0.2–) 0.5–1.2
Lemma, abaxial surface	subglabrous	not seen	usually glabrous	pubescent	glabrous
Palea					
sulcus	strigillose	not seen	puberulent	pubescent	pubescent
wing width (mm)	1–1.2	not seen	0.8–1.2	0.8–1	(1–)1.8–2.5
Fruit type	dry caryopsis	not seen	dry caryopsis	dry caryopsis	fleshy caryopsis
Geographical distribution	Colombia	Bolivia	Brazil	Peru	Peru, Bolivia, Brazil, Colombia Ecuador, Guyana, Surinam & Venezuela

when present deciduous, the sheaths adaxially pubescent and bearing fimbriae at the summit, the overlapping margin conspicuously ciliate. **Pseudospikelets** 2–4 × 0.4–0.7 cm, linear-lanceolate, straight to slightly curved, green when young becoming stramineous, consisting of a subtending bract, a prophyll, 1–4(–5) gemmiparous bracts, 1–2 sterile lemmas, 5–7 functional florets, terminating in a rudimentary anthecium; **prophylls** 4 × 2 mm, with the 2 keels winged, the sulcus membranaceous, abaxially glabrous except sericeous at the tip and strigillose along the keels, the enfolding margins glabrous and shiny, except strigillose along the keels, with the margins ciliolate, the wings 0.2–0.3 mm wide, pubescent on both sides, conspicuously ciliate on the margin, the cilia up to 0.5 mm long; **gemmiparous bracts** 1–4(–5), 5–9 × 3–6 mm, 7–11-nerved,

ovate to ovate-lanceolate, deciduous, adaxially shortly pubescent toward the upper third, otherwise glabrous and shiny, abaxially sparsely pubescent, with the midnerve strongly marked, the apex mucronate, the mucro 0.5–0.7 mm long, the overlapping margin conspicuously ciliate, the underlapping one minutely ciliolate except basally; **sterile lemmas** 1–2, 6.5–8 × 5–6 mm, 10–16-nerved, ovate-lanceolate, stramineous, slightly lighter in color than the lemmas, mucronate, the mucro 0.5 mm long, abaxially glabrescent, adaxially pubescent on the upper ½, being densely pubescent toward the apex, the overlapping margin minutely ciliolate, the underlapping one smooth, enclosing a rudimentary palea or not; **rachilla segments** 3–4.5 mm long, shortly pubescent except at the most lower portion, with a rim of hairs at the uppermost portion, disarticulating below the attachment of each lemma and falling attached to the floret. **Fertile florets** 5–7, 10–11 × 2–4 mm, with the winged palea keels exceeding the lemma margins, the lemma exceeding the palea apically only by the mucro; **lemmas** 9–11.5 × 6–8 mm, 16–18-nerved, ovate-lanceolate, green when young with purplish margins, becoming stramineous, abaxially glabrous, except with a patch of very short hairs dorsally, and a purplish-tinged to darker color line along the margins, adaxially pubescent on the upper half otherwise glabrous, the apex mucronate, the mucro 0.5–1 mm long, the margins smooth, papery; **paleas** 9–11 × 4–5 mm, stramineous, the apex acute, the sulcus 2 mm wide, 3–4-nerved, strigillose, covered by transparent, short, appressed hairs, the enfolding margins 2–3-nerved, glabrous, the margins smooth, the keels winged, the wings 1–1.2 mm wide, wider apically than basally, 2-nerved, purplish to stramineous, abaxially glabrous and shiny, adaxially strigillose along the sulcus and apically, otherwise glabrous and shiny, not prolonged at the apex, the margins ciliolate on the upper half, basally sparsely ciliolate. **Lodicules** 3, 2.5–5 × 0.7–1.8 mm, 8–12-nerved basally, membranous, acute, the upper half puberulous and thinner, covered by hyaline prickles, basally glabrous, thickened, nerved and darker, the margins sparsely ciliolate at the tip, the anterior pair slightly asymmetrical, the posterior one symmetrical, narrower than the anterior pair. **Stamens** 6, the anthers 4–5.2 × 0.1–0.5 mm, brown, basally sagittate, apically apiculate, the filament free, up to 2 mm long. **Ovary** (1.5–)2–3 × 0.4–0.5 mm, fusoid, the basal half receptacle-like, 0.7–1 × 0.5 mm, glabrous, brown, the upper half cone-shaped, 1–2 × 1 mm, densely antrorse-hispidulous, stramineous; **style** 2–2.5 mm long, densely antrorse-hispidulous, darker than the ovary, stigmas 3, plumose, ca. 5 mm long. **Fruit** 7–9 × 3 mm, an asymmetric fusoid caryopsis, with a persistent hispidulous style base at the apex, shiny and glabrescent immediately below the style, the basal two-thirds minutely strigillose, opaque, glaucous; **embryo** 1.5 × 1 mm, circular, lateral at the base of the caryopsis.

Etymology.—The specific epithet refers to the evidently canescent abaxial surfaces of the culm leaf sheath when young.

Distribution and habitat.—This species occurs in southern Colombia, in the departments of Caqueta and Putumayo, in the foothills of the eastern side of the Cordillera Oriental de los Andes, at elevations between 280–1200 m. It grows in the interior of very humid mountain forests, along creeks, but does not form dominant clumps and is generally uncommon.

Common name.—*Guadúa* (with accent).

Uses.—Farm fences and light rural infrastructure.

Phenology and Fruiting.—The flowering behavior of bamboos is still unexplained and mysterious. The factors that switch a bamboo plant from a vegetative to a flowering state are not fully understood (Janzen 1976; Judziewicz et al. 1999). *Guadua incana* can flower continuously for at least 2–3 years and without dying. A flowering culm in this species is leafy and the production of fruit and seedlings is uncommon. As in *G. weberbaueri*, only a few culms from the whole clump flower at any given time. Despite this research, it is still impossible to establish its regular flowering cycle, but we know that it takes at least more than 14 years.

The production of mature fruit in *G. incana* is scarce. Only one fruit was found in a functional floret from the middle part of the pseudospikelet. This floret falls along with the rachilla, lemma and palea attached to the base as in other *Guadua* species, e.g., *G. chacoensis* (Rojas) Londoño & Peterson (Londoño & Peterson 1992). The dorsal surface of the fruit has a conspicuous linear hilum, purplish in color, extending down the

length of the fruit and the ventral surface has a prominent embryotegium. The embryo is 1/5–1/6 of the length of the whole fruit, and is located at the base of the ventral surface. The indument of the fruit is very peculiar, with the upper 1/9th nitid; otherwise, the fruit is strigillose and covered with a whitish waxy coating.

Pseudospikelet.—The pseudospikelet is a synapomorphy for *Guadua* + *Eremocaulon* within the subtribe Guaduinae (Ruiz et al., in press), and among Neotropical woody bamboos is also found only in the genera *Elytrostachys* McClure, *Alvimia* Soderstrom & Londoño, and *Atractantha* McClure, all of them in the subtribe Arthrostylidiinae. The term is used to describe synflorescences of woody bamboos that rebranch to produce successive orders of spikelets (McClure 1966; Judziewicz et al. 1999; Young & Judd 1992, Bamboo Phylogeny Working Group 2005). According to Londoño and Clark (2002b) the following structures are all homologous at some level: subtending bracts, gemmiparous bracts, glumes, and both sterile and fertile lemmas. However, this is not the case with the prophyll, which is homologous to the palea (Stapleton 1997; Bamboo Phylogeny Working Group 2005). In *G. incana*, the most proximal bract to the prophyll gives the impression of being the prophyll itself, because the midnerve is similarly keeled and conspicuously asymmetrical, the apex bifurcate and shortly mucronate, and always fertile, enclosing a bud (Fig. 1: H–I). The prophyll when present is conspicuously ciliate but frequently the hairs rub off *in situ*.

Affinities.—*Guadua incana* is most similar to *G. weberbaueri* Pilger and *G. sarcocarpa* Londoño & Peterson. The three species share the following characters: a) triangular culm leaves with the margins slightly discontinuous at the junction with the blade; b) culm leaf blades 1/4 to 1/5 as long as the sheaths, adaxially pubescent and with a strong mucro at the apex; c) adaxial surfaces of the lemmas pubescent on their upper halves; d) paleas with pubescent sulcuses; e) conspicuous winged keels more than 0.8 mm wide and ending in an acute apex; f) lodicules strigilllose in the upper third; and g) ovaries and styles antrorse-hispidulous.

However, *G. incana* differs from *G. weberbaueri* and *G. sarcocarpa* in having (1) blade and sheath of the culm leaves conspicuously distinguished by color and pubescence (vs. inconspicuously distinguished by color and pubescence); (2) subglabrous adaxial surfaces of the leaf blades (vs. entirely glabrous); and (3) strigillose sulcus of the palea (vs. pubescent) (Table 1).

Guadua incana differs from *G. sarcocarpa* in its (a) culms erect at base, arching apically (vs. erect at base, then branching above and reaching over trees for support); (b) white-greenish and hairy culm leaves when young, (c) conspicuously ciliate overlapping margin of the foliage leaf sheaths, (d) shorter and narrower pseudospikelets, (e) the winged palea keels marginally ciliolate, and (f) dry caryopsis fruit. It differs from *G. weberbaueri* in its (a) longer pseudospikelets, (b) smooth and papery margins of the lemma, (c) abaxially glabrous but basally sparsely ciliolate winged palea keels (Table 1).

Guadua incana and *Guadua tagoara* share (a) ciliate foliage leaf sheath margins, (b) similar pseudospikelet size, (c) gemmiparous bracts with the midnerve strongly marked, (d) the lemma margins exceeded by the winged-keels of the palea, (e) a palea with two conspicuous winged-keels and a pubescent sulcus between nerves; and (f) a fusoid antrorse-hispidulous ovary (Table 1).

According to the molecular analysis done by Marulanda et al. (2002), *G. incana* shows a wide genetic distance in relation to *G. angustifolia* and greater genetic similarity with *G. amplexifolia* which shares a canescent indument on the abaxial surfaces of the culm leaf sheaths, the inner ligule extending from margin to margin and the strong mucro at the apex of the culm leaves; DNA isolation for *G. weberbaueri, G. sarcocarpa* and *G. tagora,* the three closely allied species, was not successful in the above mentioned research.

Additional specimens examined. **COLOMBIA. Caquetá:** Km 26.7 vía Florencia–Guadalupe, Quebrada La Rebolcosa, vertiente oriental de la Cordillera Oriental, 750 m, 10 Feb 1987, *Londoño & Quintero 144*; cultivated, Jardín Botánico Juan Maria Céspedes, Plot #3 collection No. XL114, 2 Jun 2004 (fl), *Londoño 982* (COL,TULV, US); Km 22 vía Florencia–Guadalupe, 670 m, 9 Feb 1987, *Londoño & Quintero 122* (TULV). **Putumayo:** Mpio. Mocoa, Vereda Suiza, carretera Mocoa-Pasto, después de La Tebaida, a orilla de Q. Suiza, 1050 m, 6 Mar 1987, *Londoño & Quintero 214* (COL, TULV, US); cultivated Jardín Botánico Juan Maria Céspedes, Plot #3 collection No. XL214, 2 Jun 2001 (fl), *Londoño 973* (TULV, US).

Guadua chaparensis Londoño & Zurita, sp. nov. (**Fig. 2**). Type: BOLIVIA. Cochabamba: Prov. Carrasco, Distrito Chapare, localidad Israel, orilla del Río Sajta, 270 m, 17° 12' 33" S, 64° 49' 47" W, 8 Aug 2004, *E. Zurita & J. Huaranca EZ 302* (holotype: BOLV; isotypes: BOL, COL, TULV, US).

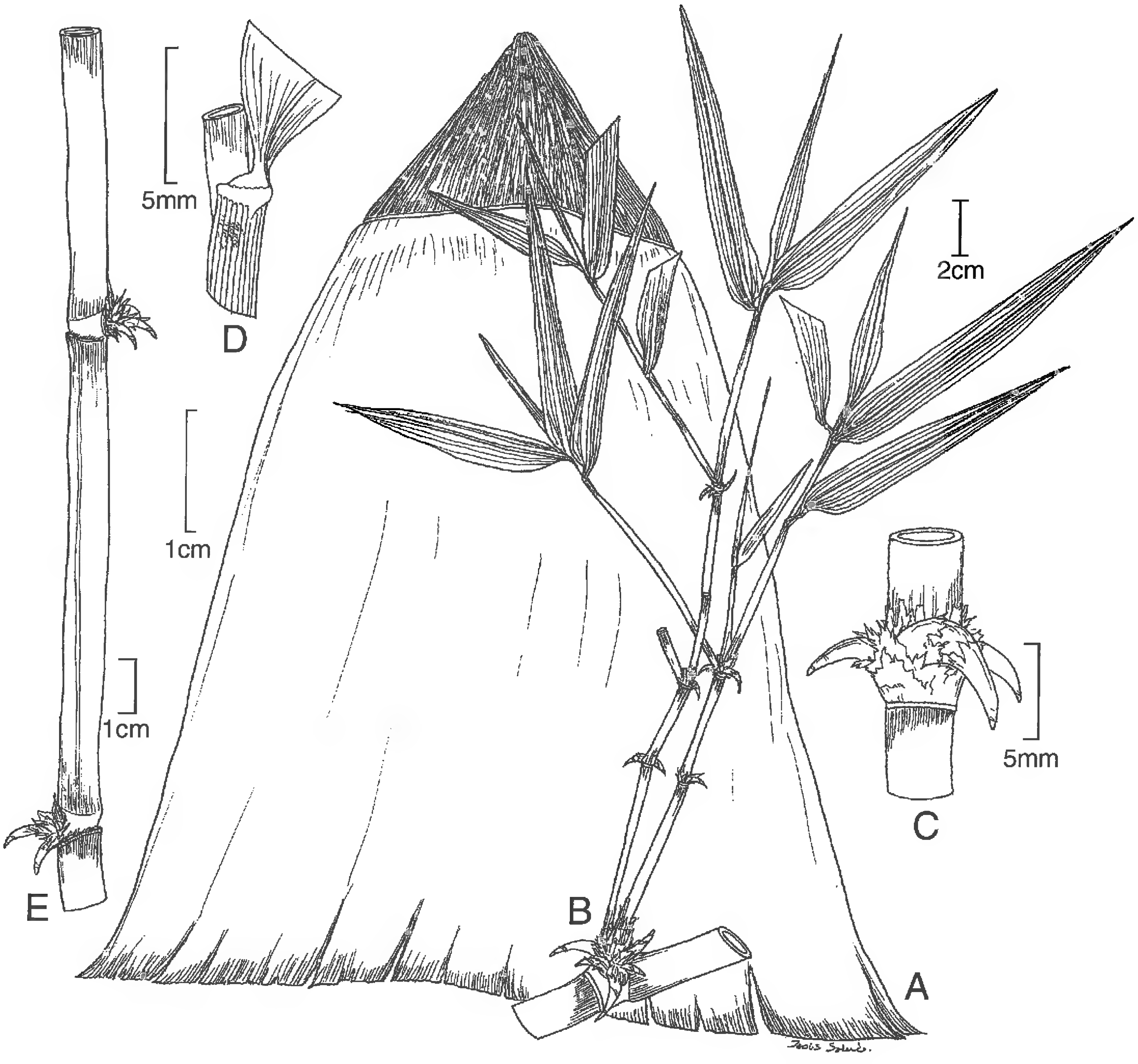

Fig. 2. ***Guadua chaparensis*. A. Culm leaf, adaxial view. B. Mid-culm node with branch compliment showing secondary branches and recurved thorns. C. Thorny branch. D. Foliage leaf ligular area, abaxial view. E. Culm segment, with thorns at the nodes (*Zurita 302*, BOLV).**

Bambusa lignosa, spinosa. Rhizomata pachymorpha. Culmi 18–25 m longi (3.5–)7–12 cm in diam.; internodia 22–70 cm longa. Folia culmorum 29–57 cm longa, 35–54 cm lata ad basim, coriacea, decidua, triangularia, vagina et lamina conspicue distinctae in juventute (vagina albido-brunnea et lanuginosa versus lamina viridis et glabrescens); vagina 23–50 cm longa; lamina (4–)9–15 cm longa, 14–17 cm lata, triangularis, erecta, viridis ad viridi-rubescentem, inflata in juventute. Folia ramorum cujusquisque complementi 5–8(–10); vagina abaxialiter subglabra, coma trichomatibus villosis secundum midnervium, prope apicem ornata, margine infera laevi et papyracea, fimbriae nullae; pseudopetiolus 2–4 mm longus; lamina (5–)15–23(–25) cm longa, (0.6–)1.3–2 cm lata, abaxialiter glabra dense papillosa et tessellata, apice acuminato. Synflorescentiae non visae. Caryopsis non visa.

Woody, thorny bamboo. Rhizomes pachymorph. **Culms** (15–)18–25 m tall, (3.5–)7–12 cm in diam., erect at base, arching from the middle to the apical portion, whitish-green when young, dark green at maturity; **internodes** 22–50(–70) cm long, cylindrical, hollow, some filled with water, the wall 1–1.5 cm thick, densely pubescent, with white hairs when young, glabrous and smooth when mature; **nodes** solitary, the nodal line horizontal, with a pubescent supranodal band 1.45–2.2 cm wide of dense, white, soft, appressed short hairs, and an infranodal band 1–2 cm wide of white, appressed hairs, the supranodal ridge pronounced; **bud** single, triangular. **Culm leaves** 29–57 cm long, 35–54 cm wide at the base, coriaceous, deciduous, triangular,

blade and sheath conspicuously distinguished by color and pubescence when young; **sheaths** 23–50 cm long, whitish-green and maculate with red when young then becoming cream-brownish to stramineous, abaxially sericeous becoming glabrous, covered when young by a single type of hairs, appressed, transparent or silky hairs up to 1 mm long, looking like wool, easily detached from the surfaces, adaxially glabrous and shiny, the margins smooth and papery; **inner ligules** 0.5–1 mm long, straight to slightly curved at the middle, extending completely from margin to margin, adaxially glabrous and shiny, abaxially canescent, the margin densely ciliate, the cilia up to 0.6 mm long, whitish or grey in color; **blades** (4–)9–15 cm long, 14–17 cm wide, 1/5 as long as the sheath, broadly triangular, erect, persistent, inflated at the central part, green to reddish-green, abaxially glabrescent, less pubescent than the sheath and different in color, adaxially densely hispid between the nerves, covered by transparent, non-appressed, stiff hairs, up to 2.5 mm long, stramineous or brownish when young becoming gray, glabrescent toward the margins, the margins papery, fimbriae to smooth, the apex mucronate, the mucro 1.2–1.5 mm long. **Branching** intravaginal, consisting of one main branch and 1 to 6 secondary branches, the branches manifestly armed, thorns (1–)3–4 per node, curved or recurved. **Foliage leaves** 5–8(–10) per complement; **sheaths** subglabrous, with a patch of hyaline, villous hairs along the midnerve near the apex, the summit glabrous, the overlapping margin conspicuously ciliate, the underlapping one ciliolate to smooth and papery; **inner ligules** 0.3–0.5 mm long, puberulous, the margin minutely ciliolate to smooth; **outer ligules** 0.2–0.3 mm long, glabrous and shiny, stramineous, the margin smooth; **pseudopetioles** 2–4 mm long, adaxially scabridulous, abaxially glabrous and pulvinate, the pulvinus yellowish, shiny; **blades** (5–)15–23(–25) cm long, (0.6–)1.3–2 cm wide, L:W = 8–13:1, 11–14-nerved, linear-lanceolate, adaxially usually glabrous, rarely bearing sparse, transparent, strigose hairs up to 1 mm long, with 3–5 raised scabrid submarginal nerves on one side, abaxially glabrous, densely papillose and tessellate, the midrib and primary nerves prominent and yellow at the middle and lower part, one margin scabrous, the other scabridulous, the apex acuminate with a mucro 1.5–2.5 mm long. **Synflorescences** not seen. **Fruit** not seen.

Etymology.—The specific epithet makes reference to the Amazon biogeographical district of the Chapare River, Cochabamba, Bolivia, where this species is found.

Distribution and habitat.—Known only from the department of Cochabamba, Carrasco, Chapare, below 900 m of elevation, with a total annual precipitation estimated to be 6000 mm and a median temperature of 25°C. It occurs along rivers and creeks, such as the Sajta and Ivirza, and is associated with *Hura crepitans* L., *Guadua sarcocarpa* Londoño & Peterson, *Mendoncia aspera* Nees, *Cecropia* sp., and *Costus* sp.

Common name.—Tacuara hembra or tacuara.

Uses.—*Guadua chaparensis* culms are used by local communities to make fences, walls, water containers, and for conducting water.

Affinities.—*Guadua chaparensis* most closely resembles *G. tagoara* (Nees) Kunth and *G. incana*. They share a culm that is whitish-green when young to dark green at maturity; cylindrical and elongated internodes 20 to 80 cm long with walls less than 15 mm thick; coriaceous culm leaves with inner ligules straight to slightly curved at the middle, abaxially with a canescent indument, looking like wool and easily detached, with the margins densely ciliate; a prominent supranodal ridge; foliage leaves in complements of 5 to 8(–10); foliage leaf sheaths bearing a patch of villous hairs along the midnerve near the apex; pulvinate pseudopetioles that are abaxially glabrous; and a prominent and yellow midnerve and primary nerves on the abaxial surfaces of the foliage leaf blades (Table 1).

Although they share several characters, *Guadua chaparensis* has a combination of vegetative features that distinguishes it from *G. incana* and *G. tagoara* even in the absence of inflorescences. The most evident ones are (a) the sericeous abaxial surface of the culm leaf sheaths, covered by one type of hair (vs. pubescent, covered by two or three different types of hair and forming a hispid surface); and (b) the absence of fimbriae at the summit of the foliage leaf sheath (vs. present) (Table 1). With respect to *G. weberbaueri* and *G. sarcocarpa*, *G. chaparensis* also shares several vegetative characters listed in Table 1.

Additional specimens examined. **BOLIVIA. Cochabamba:** Prov. Carrasco, localidad Israel, 270 m, 17° 14' 56" S, 64° 51' 84" W, 270 m, 5 May 2004, *Zurita & Baldelomar EZ176* (BOL, CUVC); al borde del camino, 270 m, 17° 12' 20" S, 64° 49' 36" W, 270 m, 4 May 2005,

Zurita & Soto EZ320 (BOL, COL); Israel, 270 m, 22 Nov 2005, *Zurita & Soto EZ324* (BOL, TULV); Proyecto Valle del Sacta, km 240 en la carretera Santa Cruz-Villa Tunari, 64° 46' W, 17° 0' S, 290 m, 12–14 Jul 1989 (-), *D. N. Smith, V. Garcia, M. Buddensiek, J. Leon & C. Negrete 13720* (MO).

Guadua weberbaueri Pilger, Feddes. Repert. Spec. Nov. Regni Veg. 1:152. 1905; *Bambusa weberbaueri* (Pilger) McClure, Smithsonian Contr. Bot. 9:68. 1973. Type: PERU. San Martín: Moyobamba, 800–900 m, "marona," *Weberbauer 4562* (holotype: B, destroyed; lectotype, here designated: MOL #00007883; isolectotype: US #79101! fragment).

Etymology.—The specific epithet refers to the German botanist and expedition leader August Weberbauer (1871–1948), who devoted his life to studying the flora of Peru.

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TETRAZYGIA PARALONGICOLLIS (MICONIEAE: MELASTOMATACEAE), A NEW SPECIES FROM THE SIERRA DE BAORUCO AND SIERRA MARTIN GARCIA, DOMINICAN REPUBLIC

Walter S. Judd & Gretchen M. Ionta

Department of Botany
220 Bartram Hall
P.O. Box 118526
University of Florida
Gainesville, Florida 32611, U.S.A.
wjudd@botany.ufl.edu

Teodoro Clase

Jardín Botánico Nacional Dr. Rafael Ma. Moscoso
Apartado 21-9
Santo Domingo, REPÚBLICA DOMINICANA
ted_clase@hotmail.com

J. Dan Skean, Jr.

Department of Biology
Albion College
Albion, Michigan 49224, U.S.A.
dskean@albion.edu

ABSTRACT

Tetrazygia paralongicollis, a new species from the Sierra de Baoruco and Sierra Martin Garcia of the Dominican Republic, is described. This species occurs in pine forests and moist montane forests from 720–860 m, and is compared with its purported closest relatives: *T. longicollis* and *T. elaeagnoides*.

RESUMEN

Se describe **Tetrazygia paralongicollis,** una nueva especie de la Sierra de Baoruco y de la Sierra Martin Garcia de la República Dominicana. Este taxon ocurre en bosques de pino y bosques montanos húmedos entre los 720–860 m de altitud, y se compara con sus presuntos parientes más cercanos: *T. longicollis* y *T. elaeagnoides*.

Key Words: Hispaniola, Dominican Republic, Melastomataceae, Miconieae, *Tetrazygia*

During the course of fieldwork conducted in connection with the study of the systematics of Miconieae (Melastomataceae), herbarium material of a distinctive species was collected in the Sierra Martin Garcia (by W.S. Judd, in 1992 and 2006) and Sierra de Baoruco (by T. Clase, in 2001). It is now evident that these collections represent an undescribed species of *Tetrazygia* (Miconieae, Melastomataceae), which appears to be closely related to *T. longicollis* Urb. & Cogn. and *T. elaeagnoides* (Sw.) DC. These plants are described here, provided with the name *T. paralongicollis*, and compared morphologically with the above mentioned species.

Recent molecular-based phylogenetic analyses (F. Michelangeli, R. Goldenberg, W. Judd, and others; unpublished data) indicate that *Tetrazygia*, a genus of ca. 20 species (Judd & Skean 1991; Liogier 2000), is not monophyletic as traditionally circumscribed. The species of *Tetrazygia* Rich. are intermixed in preliminary cladograms with members of several other genera of Miconieae, especially *Pachyanthus* A. Rich. and *Calycogonium* DC., two genera that are predominantly Antillean in distribution, as is *Tetrazygia*. Clarification of generic limits within this subclade of the Miconieae, i.e., an Antillean complex (see Michelangeli et al. 2004, 2008) is beyond the scope of this paper, but we note that *T. elaeagnoides*, which has 4-merous flowers (as does *T. longicollis* and the species described herein), in preliminary cladistic analyses does not appear to be closely related to the species with 5- or 6-merous flowers, such as *T. bicolor* (Mill.) Cogn., *T. coriacea* Urb., and *T. lanceolata* Urb.

Tetrazygia paralongicollis Judd, Ionta, Clase & Skean, sp. nov. (**Fig. 1**). Type: DOMINICAN REPUBLIC. Pedernales Prov.: Sierra de Bahoruco, 18 km al Este de Cabo Rojo, en la carretera hacia Aceitillar, bosque de transición con *Pinus occidentalis*. Lat. 71° 37' 63" W, Long. 18° 6' 7" N, 720 m, 19 Jul 2001 (fl, fr), *T. Clase & P. Delprete 3035* (holotype: JBSD; isotypes: FLAS, NY, S).

Species haec ab *Tetrazygia longicollis* Urb. & Cogn. differt trichomatibus globosis-stellatis (vs. trichomatibus complanatis-stellatis), veins tertiariis plerumque per veins quaternariis connexis (vs. plerumque per veniis composite-intertertiariis separatis), et calyce lobis externis ca. 1.2 mm longis (vs. 1–5 mm longis).

Shrub or small tree to 6 m tall, with gray, horizontally furrowed bark; lateral branches arising from the main trunk ± horizontally, then arching upward. Indumentum of multicellular, pale-ferrugineous, nearly sessile to long-stalked, globular-stellate hairs, and often also simple, elongate multiseriate hairs 0.6 to 1.4 mm long, these sometimes with minute antrorse bristles. Young twigs 2–5 mm wide, slightly quadrangular, with the interpetiolar face (in relation to the distally adjacent node) slightly concave, the adjacent sides slightly convex, becoming terete with age, with moderate to dense globular-stellate hairs and often sparse simple, elongate multiseriate hairs, many breaking off with age; internodes 1.1–6.1 cm long (to 8.5 cm in vigorously growing vegetative shoots). Leaves with petiole 6–9.4 mm long, (but to 28 mm in leaves of vigorously growing vegetative shoots), with dense globular-stellate hairs; blade 2.5–6.8(–20.4) cm long, 0.6–2.2(–7.7) cm wide, 3.1–4.2 (2–3.5 in leaves of vigorously growing sucker-shoots) times longer than wide, ovate to elliptic, flat, coriaceous, the apex acute to acuminate, with the tip of the leaf with upturned margins, forming a mucro 0.5–1.1(–6) mm long with adaxial pocket, the base narrowly acute to cuneate or slightly cordate, the margin plane to slightly revolute, nearly entire, i.e., with only a very few teeth along distal portion of blade, and these at most 0.1 mm long, to ± clearly serrulate or ciliate-serrulate, with teeth 0.1–0.3 mm long, sometimes associated with a short multiseriate hair, ± evenly spaced along margin; venation acrodromous, basal to suprabasal, with prominent midvein and 4 secondary veins (6 in leaves of rapidly growing vegetative shoots), 2 conspicuous secondary veins positioned 1.7–4(–16 in sucker-shoot leaves) mm from margin, and 2 inconspicuous secondary veins closer to margin (but sucker-shoot leaves with an additional pair of inconspicuous, ± intramarginal, secondary veins), numerous percurrent tertiary veins oriented subperpendicular to midvein, the tertiary veins occasionally separated by composite-intertertiary veins (but such veins more common on leaves of sucker-shoots), the higher-order veins reticulate; adaxial surface green, initially with numerous globular-stellate hairs, but quickly glabrescent, the midvein and major secondary veins moderately impressed, minor secondary and tertiary veins slightly impressed to flat, and higher order veins flat, the surface appearing minutely papillose after drying due to presence of numerous subglobose subcuticular druse crystals; abaxial surface light green, with dense pale ferrugineous, globular-stellate hairs obscuring the epidermal surface, and sometimes also elongate, multiseriate hairs, some stellate hairs on the major veins darker ferrugineous, the midvein prominently raised, major secondary veins moderately raised, minor secondary veins, tertiary veins, and some composite-intertertiary veins slightly raised, and higher-order veins flat (or very slightly raised in some leaves of sucker-shoots). Inflorescences 3- to 12-flowered pyramidal cymes of 1 to 2 branch-pairs, 4–7.5 cm long, 1.7–5 cm in diameter; proximal segment of lowermost inflorescence branches 1.4–2.5 cm long, distal internodes of inflorescence branches increasingly shorter, ultimate branches 1.1–1.9 cm long, and flowers appearing in 1- to 3-flowered dichasia, with dense globular-stellate hairs and sparse elongate multiseriate hairs; peduncle 0.5–2.1 cm long, with similar indumentum; proximal inflorescence branch associated with pair of persistent leaflike bracts, 2.5–4.3 cm long, 0.7–1.2 cm wide, similar in form to vegetative leaves, other inflorescence branches associated with pair of caducous bracts (and not present on specimens examined). Flowers perfect, zygomorphic (due to androecium form), with pedicel 1.4–1.5 mm long, the indumentum similar to that of inflorescence branches. Free portion of hypanthium slightly constricted above ovary, flaring and funnelform distal to the constriction, 2.9–3.8 mm long, outer surface with dense to moderate globular-stellate hairs and sparse elongate multiseriate hairs, the inner surface slightly 16-ridged, glabrous except for occasional minute-globular hairs on the ridges. External calyx lobes 4, ca. 1.2 mm long, ca. 0.8 mm wide, narrowly triangular, with acute apex, and terete in cross section, with dense globular-stellate hairs; internal calyx lobes 4, 0.6–0.8 mm long, 2.9–3.4 mm wide, broadly triangular, apex rounded, green to red-tinged, with dense globular-stellate hairs abaxially, glabrous adaxially, the margin membranaceous, minutely erose; calyx tube ca. 1.5 mm long. Petals 4, imbricate in bud, ± asymmetrical, ovate-obovate, 5.2–6.1 mm long, 4.3–4.9 mm wide, glabrous, white; apex rounded; margin entire. Stamens 8, anther elongate-ovate, 4.6–5.2 mm long, glabrous, pale yellow, very

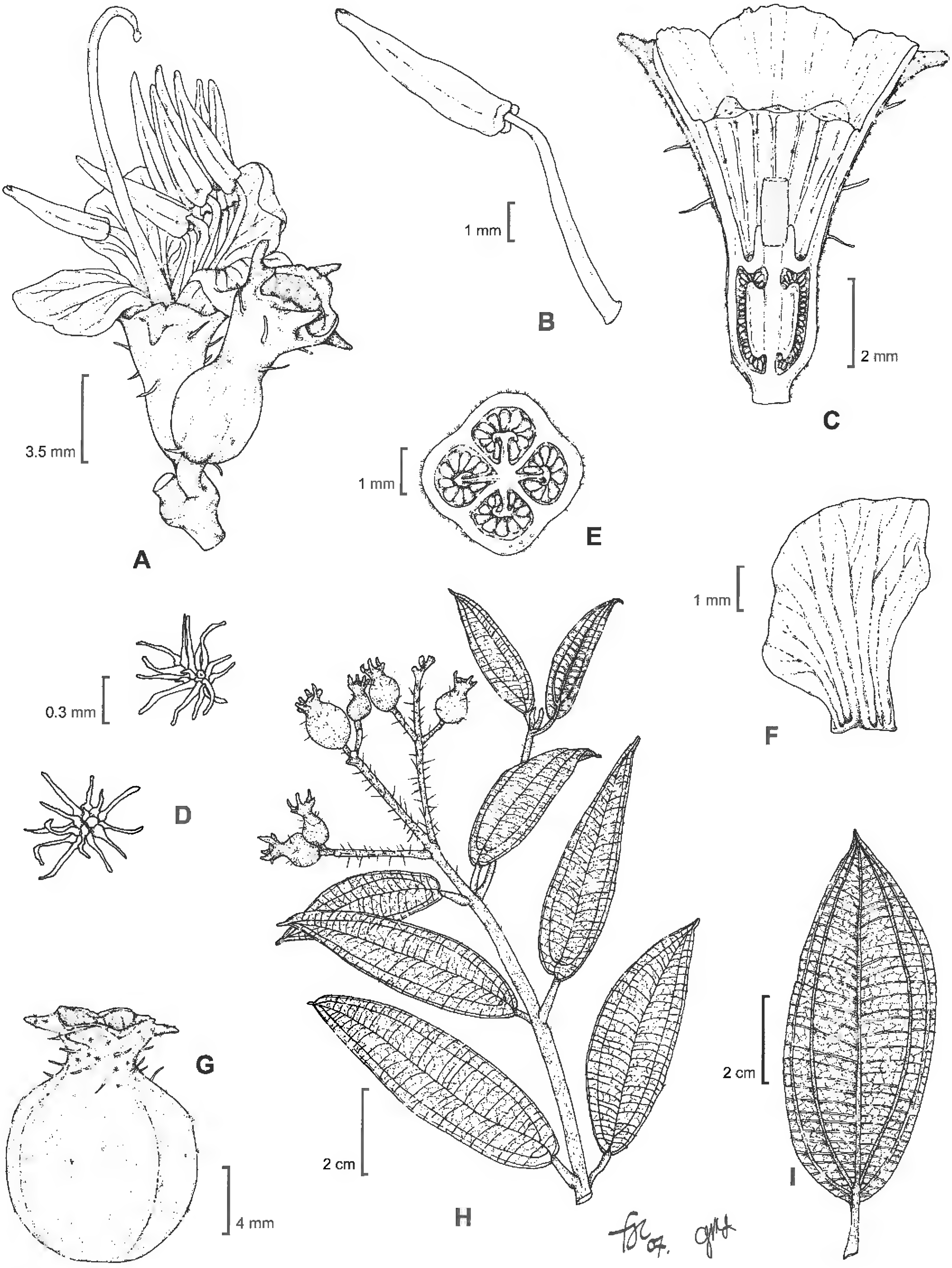

Fig. 1. A–I. *Tetrazygia paralongicollis*. **A.** Dichasium, with one flower removed. **B.** Stamen. **C.** Ovary and hypanthium, in longitudinal section. **D.** Stellate hairs, from abaxial leaf surface. **E.** Ovary, in cross-section. **F.** Petal. **G.** Berry. **H.** Habit. **I.** Leaf, abaxial surface. (All illustrations drawn from holotype, except for "I" which is from *Judd 8148* (FLAS)).

slightly sagittate at base, fertile the entire length, and opening by a single dorso-apical pore, the filament terete, 5.8–6 mm long, glabrous, white. Ovary 4-loculate, ca. 4/5 inferior, ellipsoidal and slightly 4-lobed, 3.5–3.9 mm long, 2.1–2.5 mm wide, with cylindrical apical crown ca. 0.7 mm long encircling base of style, the crown slightly 8-ridged, with sparse stellate hairs and elongate-uniseriate hairs at apex; style ca. 15 mm long, terete, glabrous. Placentation axile with placentas inserted into locules with narrowed longitudinal placental stalk with flattened ellipsoid distal portion, T-shaped in cross-section; ovules numerous. Nearly mature berries 9–12 mm in diameter, globose-ellipsoid, with strongly constricted persistent hypanthium, green when immature, but probably turning purple-black at maturity, with sparse globular-stellate hairs. Seeds angular-obovoid, 0.7–0.9 mm long; testa ± smooth.

Distribution and habitat.—*Tetrazygia paralongicollis* is restricted to the southern part of the Dominican Republic where it has been collected only in the Sierra de Baoruco and Sierra Martin Garcia (Fig. 2), from 720–860 m. In the Sierra de Baoruco it occurs in *Pinus occidentalis* Sw. forests, while in the Sierra Martin Garcia it grows in moist montane forest (on limestone). In the Sierra Martin Garcia, associated melastomes include *Calycogonium hispidulum* Cogn., *Miconia laevigata* (L.) DC., *Sagraea fuertesii* (Cogn.) Alain, *Tetrazygia elaeagnoides* (Sw.) DC., and *T. longicollis* Urb. & Cogn.

Etymology.—The specific epithet highlights the purported close relationship of this species with *Tetrazygia longicollis*, especially as evidenced in the characteristics of its flowers and fruits.

Vegetative anatomy.—Stem, leaf, and petiole anatomy were assessed in material of *Tetrazygia paralongicollis*, i.e., *Judd 8148* (FLAS) and *Clase & Delprete 3035* (FLAS), and leaf and petiole anatomy were assessed in material of *T. longicollis*, i.e., *Judd 6656* (FLAS) and *T. elaeagnoides*, i.e., *Judd 6553* (FLAS) using the phloroglucinol-hydrochloric acid technique outlined by Howard (1974). As is typical of Melastomataceae, the stems of *T. paralongicollis* have a ring of xylem with phloem positioned both externally and internally (amphiphloic), and as characteristic of Miconieae, medullary vascular bundles are present. The pith is lignified, and perivascular fibers are lacking, but there are scattered lignified idioblasts in the inner portion of the cortex, which may have a protective function (because they surround the stele). Druses also are present in the cortex. The nodes are unilacunar/unifascicular, but the vascular bundle divides within the petiole base, forming several bundles in the petiole. The petioles (sectioned at their midpoint) of all three species exhibit a U-shaped pattern composed of 7 to 11 vascular bundles, with the individual bundles composed of xylem surrounded by phloem. The ground parenchyma is unlignified, but in *T. paralongicollis* there are a few scattered lignified idioblasts, and in *T. longicollis* there are numerous lignified idioblasts. The petioles of *T. elaeagnoides* lack lignified idioblasts, but have abundant druse crystals; the parenchyma is literally packed with druses. In contrast, the parenchyma of *T. paralongicollis* and *T. longicollis* has only scattered druse crystals. The leaves of all three species have dorsoventral blades with an epidermis, palisade and spongy mesophyll; the midvein has several vascular bundles, which are more or less arranged in a ring. Lignified idioblasts are present in the parenchyma associated with the midvein vascular bundles of *T. paralongicollis* and *T. longicollis*, while these cells are lacking in *T. elaeagnoides*. The abaxial leaf surface of all three species is covered with a thick layer of stellate hairs, which are variably lignified. As with the petiole, the parenchyma of the midvein of *T. elaeagnoides* contains very abundant druses. Druses are present in the lamina of all three species, with these crystals placed below the epidermis in either the palisade or spongy mesophyll.

Additional collections. **DOMINICAN REPUBLIC. Azua Prov.:** Sierra Martin Garcia, Loma del Aguacate, hills and ridge of mountain west of Barreras, ca. 850–860 m, plants collected along trail from Barreras to El Copey, 17 May 1992 (sterile), *Judd 6552* (FLAS, JBSD); Sierra Martin Garcia, hills and ridges of mountain SW of Barreras, along trail from Barrera toward El Copey (from N side of town, trail starts to NNW, cuts W, then SW, then S, then more or less W, with variance); near Barahona, 810–820 m. Lat. 18° 19' 4.4" N, Long. 70° 56' 47.2" W, Datum: WGS84, 6 Jun 2006 (sterile), *Judd 8147* (FLAS, JBSD, MICH, MO, MSC, NY, S, US)

DISCUSSION

Tetrazygia paralongicollis is most similar to *T. longicollis* (incl. *T. brevicollis* Leonard). This is especially seen in the form of its flowers and fruits, i.e., 4-merous, with conical-terete external calyx lobes, broadly triangular internal calyx lobes, ovate-obovate, white petals, stamens with ovate-elongate anthers, an ellipsoidal

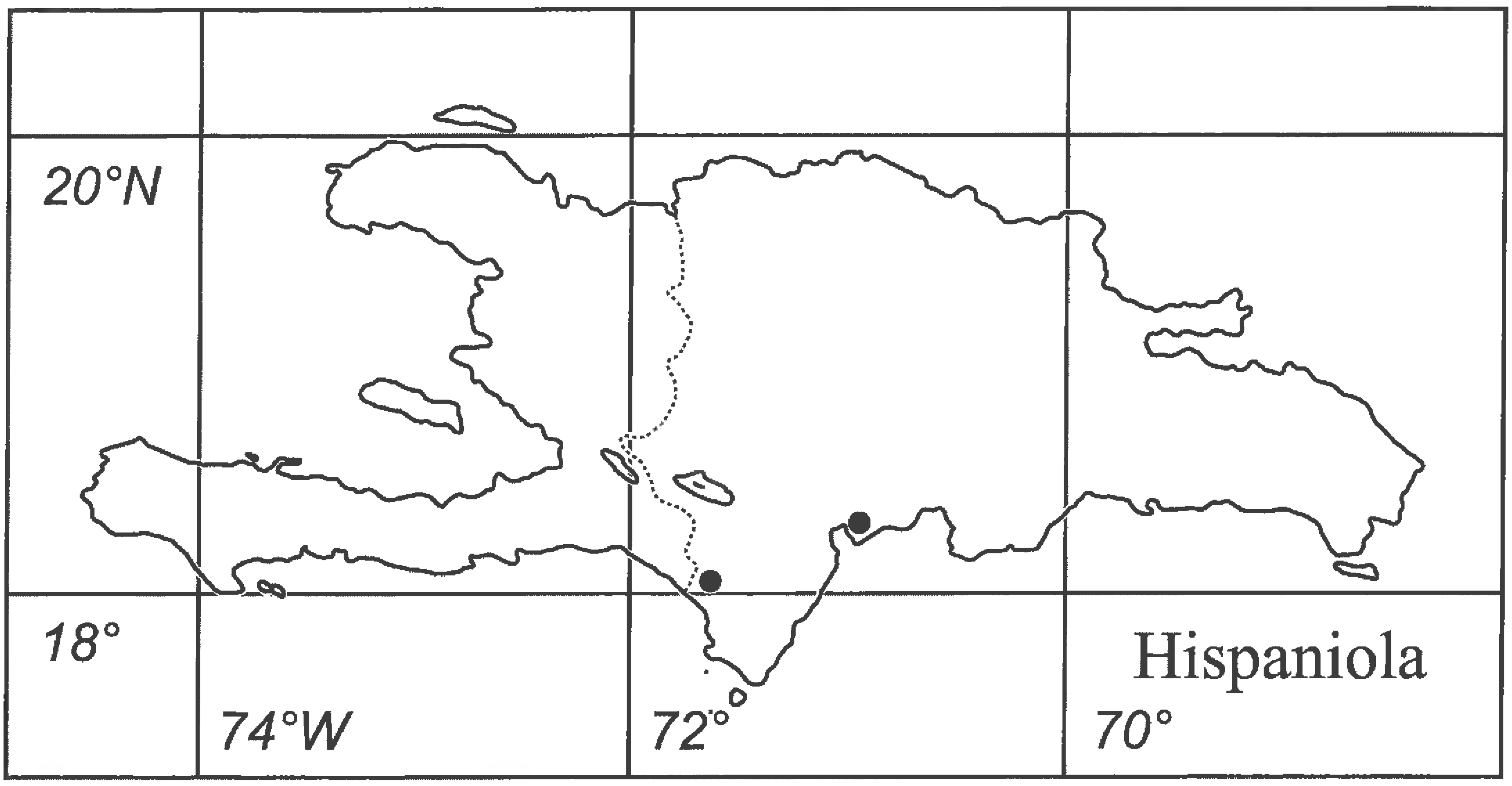

Fig. 2. Distribution of *Tetrazygia paralongicollis* (dots).

ovary (only slightly 4-lobed) and with the placentas inserted into locules, T-shaped in cross section, and globose-ellipsoid berries with strongly constricted hypanthium. However, it is consistently differentiated from *T. longicollis* by its globose-stellate hairs, i.e., with branches radiating in all directions from a globose central region (vs. flattened-stellate hairs, i.e., with branches more or less radiating outward from a central region), the tertiary veins usually connected by reticulate quaternary veins, i.e., only occasionally separated by composite-intertertiary veins (vs. tertiary veins usually separated by composite-intertertiary veins, thus making the leaf "tertiary" veins appear to be closer together than they actually are), and external calyx lobes that are ca. 1.2 mm long (vs. variable in length, ca. 1–5 mm long). *Tetrazygia paralongicollis* is also quite similar to *T. elaeagnoides*, especially in the morphology of its stellate hairs and in the pattern of venation of its leaves. *Tetrazygia paralongicollis* is easily distinguished from this species by its hypanthia (and fruits), which are globose-ellipsoid and only very slightly 4-lobed when in flower, becoming unlobed in fruit (vs. subglobose and strongly 4-angled), placental form, i.e., the placenta extended into the locule and T-shaped in cross-section (vs. elliptic in cross-section), and the presence of lignified idioblasts in the parenchyma of the petioles (vs. lignified idioblasts lacking). In addition, many plants of *T. elaeagnoides* have shorter external calyx lobes, e.g., ca. 0.2–0.4 mm long, but in some plants they may be as long as 1.6 mm. Plants of *T. paralongicollis* from the type locality differ from both of these species in having simple, elongate, multiseriate hairs intermixed with the globular-stellate hairs on their stems, abaxial leaf surface, leaf margin (in association with the teeth), inflorescence axes, and hypanthium. The plants of the Sierra Martin Garcia, however, lack these hairs, but these plants (unfortunately, only collected in sterile condition) are considered within *T. paralongicollis* because their leaf shape, venation, and stellate-hair morphology closely match that of the type specimens. It is noteworthy that the leaves of the Sierra Martin Garcia population are frequently larger than those of either *T. longicollis* or *T. elaeagnoides*. This new species occurs with both *T. longicollis* and *T. elaeagnoides* in the Sierra Martin Garcia, but no intermediate plants were seen in that region. Only *T. longicollis*, however, is known from the Sierra de Baoruco, in the vicinity of the type locality.

Tetrazygia paralongicollis, exhibiting a distinctive combination of morphological characters, satisfies the expectations of the morphological-phenetic (Judd 2007) and diagnostic (Wheeler & Platnick 2000) species concepts.

The description of *Tetrazygia paralongicollis* brings the number of species of *Tetrazygia* known from

Hispaniola to eight (Liogier 2000), given that we consider *T. urbaniana* (Cogn.) Croizat ex Moscoso to be a synonym of the morphologically variable *T. tuerckheimii* (Cogn.) Ekman & Urb. All the other species of *Tetrazygia* show fairly broad geographical distributions on the island compared to *T. paralongicollis*.

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UNA NUEVA ESPECIE DE *CUATRESIA* (SOLANACEAE) DE COSTA RICA Y PANAMÁ

D. Armando Soto
Instituto Nacional de Biodiversidad (INBio)
Apdo. 22-3100, Santo Domingo de Heredia
COSTA RICA
asoto@inbio.ac.cr

A.K. Monro
The Natural History Museum (BM)
Cromwell Road London, SW7 5BD
UNITED KINGDOM
a.monro@nhm.ac.uk

ABSTRACT

Cuatresia amistadensis, a new species from Costa Rica and Panamá is described and illustrated, and its taxonomic relationships are discussed.

Key Words: Solanaceae, *Cuatresia*, Talamanca, Parque Internacional La Amistad, Costa Rica, Panamá.

RESUMEN

Cuatresia amistadensis una nueva para Costa Rica y Panamá, es descrita e ilustrada, y se discuten sus relaciones taxonómicas.

Palabras Clave: Solanaceae, *Cuatresia*, Talamanca, Parque Internacional La Amistad, Costa Rica, Panamá.

La familia Solanaceae se distribuye en áreas templadas, tropicales y subtropicales, pero su mayor representación se encuentra en el trópico, con ca. 95 géneros y 2200 especies (Nee 2004). El género *Cuatresia* Hunz. (Hunziker 1977) de origen Neotropical, posee 12 especies publicadas y 6 para Costa Rica (A.Soto en prep.) se distingue del género *Witheringia* L'Hér. por sus anteras ventrifijas y pedicelos no articulados (Hunziker 1987); un carácter importante de notar es que el género *Cuatresia* se distingue de otros géneros relacionados por su patrón de estivación induplicada (N. Sawyer, com. pers.).

En el trabajo de campo para el proyecto 'Baseline tools for management in PN La Amistad (Costa Rica/Panama)', realizado en el Parque Internacional La Amistad entre Costa Rica y Panamá, se recolectó la siguiente especie de *Cuatresia*, la cual es descrita a continuación.

Cuatresia amistadensis D.A. Soto & A.K. Monro, sp. nov. (**Fig. 1**). Tipo. COSTA RICA. Limón: Cantón de Talamanca, Parque Internacional La Amistad, camp 1, Río Lori, secondary forest adjacent to camp, 17 Feb 2007, *A.K. Monro & D. Santamaría 5425* (holotipo: INB, isotipos: BM, MO, PMA).

Planta glabra foliis oblongo-ellipticis vel ellipticis, 12.5–21 cm longis et 5–10.5 cm latis, dimidiatis. Inflorescentia cymosa axillaris, pedunculis 3,8–12 cm. Corolla pentamera, campanulata, 7–20 mm longa, lobis oblongo-obtusis, 3–5 mm longis, filamentis 1 mm longis, et tubo corollae ad medium affixo. Gynoecium 6–10 mm. Fructus globosus, 8–12 mm longus.

Arbustos terrestres, ocasionalmente epífitos, hasta 4 m de altura. Ramitas glabras, rojo palido–marrón, tallos principales con nudos engrosados, tallos con hojas con una constricción arriba del nudo, internudos 2,8–8 cm de largo, 2,5–6 cm de ancho. Hojas oblicuas y en pares desiguales, por lo general las hojas menores 4 a 8 veces más pequeñas que las mayores; hojas mayores oblongo elípticas a elípticas, 12,5–21 × 3,5–8.8 cm; hojas menores 0,9–65 cm × 0,6–36 cm de ancho; el margen poco ondulado y repando, de un color café claro a anarajado-amarillento especialmente en el envés hacia la vena central, glabras en ambas superficies y un poco escabrosas hacia los márgenes, con pequeñas escamas blanquecinas-cremosas, bases agudas, obtusas y asimétricas, ápice largamente acuminado, peciolos 3–9 mm de largo 1–1,5 mm de ancho. Inflorescencias péndulas de 9–20cm de largo con 2 a 19 flores en 2–3 dicasios, pedúnculos 3,8–12 cm, de menos de 1mm de diámetro, glabros y angulados. Flores con pedicelos de 8–16 mm, obcónicos, menos de 1 mm ancho proximalmente hasta 3 mm distalmente; cáliz glabro, hipocrateriforme de 2–3 mm de largo, ligeramente acostillado donde cada costilla finaliza en un lóbulo apenas perceptible; corola verde campanulada, 7–20 mm de largo, 5-lobada en 1/2 a 2/3 de su extensión, lobos, oblongo-agudos y cuculados, con venación evidente, 3–5 mm de largo, ciliolados en los márgenes induplicados, más largos que el tubo, filamentos 1 mm de largo, fusionados a la corola por la mitad de su longitud, glabros; anteras basifijas, 2 mm de largo, no apiculadas;

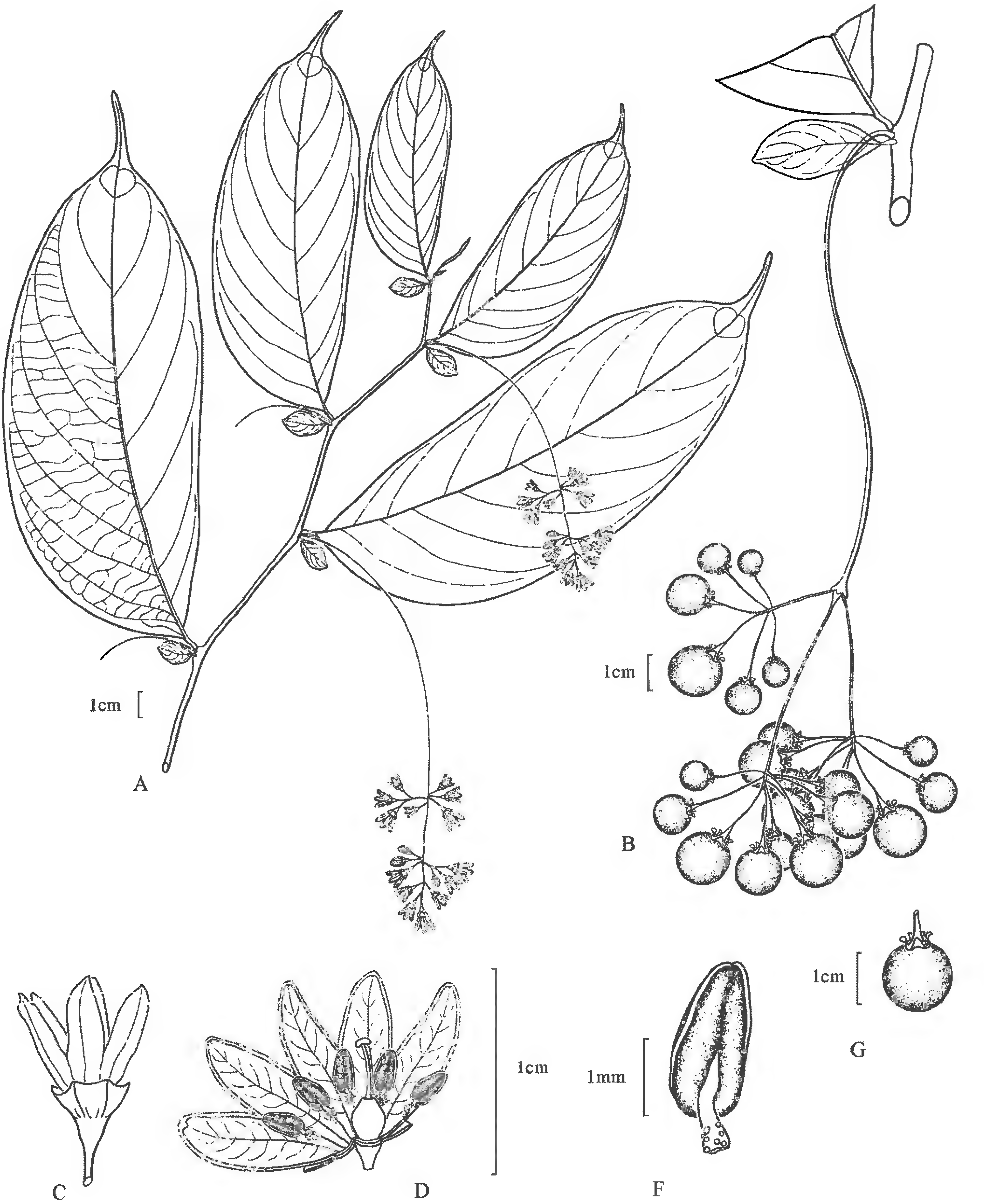

Fig. 1. Ilustración de *Cuatresia amistadensis*. A. Rama florífera, B. Infrutescencia, C. Flor, D. Corola abierta, F. Antera, G. Fruto.

pistilo 6–10 mm; estilo apical y estigma claviforme. Frutos 8–12 × 7,5–12 mm, redondeados, cáliz no acrescente. Semillas 2,5–3 mm de diámetro, discoides, de color pardo claro con la superficie foveolada.

Distribución, hábitat y ecología.—Bosques muy Húmedos y nubosos, bosques primarios y secundarios, principalmente en la vertiente Caribe, más escasa en el pacífico, al Sur de la Cordillera de Talamanca, en Costa Rica y Panamá, entre 980–2050 m.

Cuadro 1. Cuadro comparativo entre *Cuatresia amistadensis, C. plowmanii, y Witheringia cuneata.*

Carácter	Cuatresia amistadensis	Cuatresia plowmanii	Witheringia cuneata
Pedúnculos	3,8–12 cm de largo, <1 mm de diámetro, angulados	4–25 cm de largo, 0,75–1 mm de diámetro, cilíndricos	0,3–6 cm de largo, 1–2 mm de diámetro, cilíndricos
Pubescencia en hojas e infl.	Hojas glabras con diminutas escamas blancas. Infl. glabras	Hojas glabras sin diminutas escamas blancas. Infl. glabras	Glabras o pubescentes, en ocasiones con domacios. Infl. puberulentas a pubescentes
Pedicelos	8–16 mm muy delgado y difícil de distinguir del cáliz	5–8 mm, muy delgado y difícil de distinguir del cáliz	3–6 mm, robusto y claramente definido del cáliz
Cáliz floral	Hipocrateriforme	Campanulado	campanulado y truncado
Corola	Lobos 3–5 mm, divididos por > 1/3 de su largo, tubo excerto del cáliz por 2–3 mm	Lobos ca. 4 mm, dividido por < 1/3 de su largo, tubo excerto del cáliz por 7–10 mm	lobos 4–8 mm muy angostos, tubo completamente inserto en el cáliz
Estambres	Filamentos glabros, 1 mm, unidos al corola por > ½ de su largo, anteras 2 mm	Filamentos piliformes, 2–3 mm, unido al corola por < ½ de su largo, anteras 2 mm	Filamentos pilosos, 1 mm, anteras 2,5–3 mm
Rango de altitud	1780–2050 msnm	0–2000 msnm	100–1900 msnm

Fenología.—Se ha recolectado con flores de Diciembre a Mayo, y con frutos de Febrero a Marzo.

Etimología.—El epíteto de este taxón está dedicado al parque internacional La Amistad, ubicado entre Costa Rica y Panamá (PILA).

Cuatresia amistadensis es fácilmente distinguible por poseer pedúnculos péndulos, muy largos y delgados, hasta 10.5 cm, además con hojas dimidiadas secando de un color café claro. Esta especie se podría confundir con *Witheringia cuneata* (Standl.) Hunz., ya que comparten un rango de distribución geográfica similar y porque tienen pedúnculos alargados, pero en *W. cuneata* son más cortos y robustos, miden como máximo 6 cm. Las diferencias entre ambos taxones se mencionan en el Cuadro 1. Otra especie muy similar es *Cuatresia plowmanii* A.T. Hunziker, que se distribuye en el Sur de Colombia y Ecuador, el largo de los pedúnculos es similar pero los lobos de la corola en *C. plowmanii* son triangulares vs. oblongo–acutados, están divididos por < 1/3 del largo de la corola vs. divididos por > 1/3 del largo; además la inflorescencia es una cima unípara vs. compuesta por dicasios y las hojas presentan una venación terciaria muy continua y conspicua, otras diferencias entre estos taxones se anotan en el Cuadro 1.

Paratipos: **COSTA RICA. Puntarenas:** Cantón de Coto Brus, Zona Protectora Las Tablas, Cuenca Térraba Sierpe, finca La Neblina, finca de William Gamboa 8°54'17" N, 82°45'03" O, 2050 m, 1 Mar 1997, *B. Gamboa 1122* (CR, INB, MO). **Limón:** Cantón de Talamanca, Parque Nacional Cordillera de Talamanca, Río Lori, cerro junto al paso del sendero de Ujarrás a San José Cabécar 9°21'25" N, 83°13'20" O, 1900 m, 22 Mar 1993 (fl) *A. Fernández 781* (CR, INB). **PANAMÁ. Bocas del Toro:** campamento de Lucho. 9° 05'052' N, 82°44'733" W. 1850 m, 19 Mar 2004 (fl) *E. Alfaro & A.K. Monro 5628* (BM, INB, PMA); La pata del Cedro, 9°04'270" N, 82°44'174" O, 1750 m, 11 Mar 2004, (fl) *A.K Monro & E. Alfaro 4302* (BM, INB, MO, MEXU, PMA); La pata del Cedro, ridgetop, 9°04' 270 N, 82°44'174" O, 1750 m, 13 Mar 2004, (fl) *A.K Monro & E. Alfaro 4379* (BM, INB, MEXU, MO, PMA); Caribbean slopes of Cerro Fabrega on slopes of 'Falso Fabrega' 9°09'54" N, 82°40'45" O, 980 m, 25 Mar 2005, *A.K Monro & S. Cafferty 4826* (BM, INB, MO, PMA). **Chiriquí:** along road between Fortuna lake and Chiriquí Grande, 4–4,5 km N of dam over Fortuna Lake, 8°43'N, 82°17' O, 1100–1135 m, 8 Mar 1985, *T.B. Croat & M.H. Grayum 60046* (BM, MO); 28 Dic 1995, *E. Montenegro & B. Cuevas 1148* (BM); 28 Dic 1995, *E. Montenegro & B. Cuevas 1185* (BM); SE slopes of Cerro Pate Macho, trail for Río Palo Alto, 4 km NE of Boquete, 1700–2100 m, 26 May 1981, *K. Sytsma et al. 4858* (BM, MO).

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TWO NEW SPECIES OF *BACCHARIS* SECT. CAULOPTERAE (ASTERACEAE: ASTEREAE) FROM SOUTHERN BRAZIL

Angelo Alberto Schneider

Universidade Federal do Rio Grande do Sul
Programa de Pós-Graduação em Botânica
Av. Bento Gonçalves, 9500, Porto Alegre
Rio Grande do Sul, 91501-970, BRASIL
angeloschneider@yahoo.com.br

Ilsi Iob Boldrini

Universidade Federal do Rio Grande do Sul
Programa de Pós-Graduação em Botânica
Av. Bento Gonçalves, 9500, Porto Alegre
Rio Grande do Sul, 91501-970, BRASIL
ilsi.boldrini@ufrgs.br

ABSTRACT

Two new species of *Baccharis* L. sect. *Caulopterae* DC. (Asteraceae) from the highlands of southern Brazil are presented, **Baccharis apicifoliosa** A.A. Schneid. & Boldrini and **Baccharis flexuosiramosa** A.A. Schneid. & Boldrini. The new species are described, illustrated and compared with the similar species, *Baccharis milleflora* (Less.) DC. and *Baccharis organensis* Baker, respectively.

RESUMEN

Dos nuevas especies de *Baccharis* L. sect. *Caulopterae* DC. (Asteraceae) que viven en regiones de altitud del sur de Brasil se presentan, **Baccharis apicifoliosa** A.A. Schneid. & Boldrini and **Baccharis flexuosiramosa** A.A. Schneid. & Boldrini. Se describen, ilustran y se compara las nuevas especies con las similares, *Baccharis milleflora* (Less.) DC. y *Baccharis organensis* Baker, respectivamente.

The infrageneric classification of *Baccharis* was recently worked for Giuliano (2001, 2005) to Argentina, Giuliano and Nesom (2003), and by Müller (2006) to Bolivia. Müller used the name "*Baccharis genistelloides* Group" for the species belonging to *Baccharis* sect. *Caulopterae*, which consists of perennial herbs, subshrubs, and shrubs with 2–3-alate stems, normal to squamiform leaves, capitula sessile and arranged in spikes or pseudospikes, female capitula without paleae, and achenes (5–20)-ribbed and glabrous or papillose. Section *Caulopterae* is restricted to South America.

During a taxonomic revision of *Baccharis* sect. *Caulopterae* of southern of Brazil two new species were recognized with morphological characteristics that distinguish them from all other species.

Baccharis apicifoliosa A.A. Schneid. & Boldrini, sp. nov. (**Figs. 1–2**). Type: BRAZIL. Rio Grande do Sul: Município de São Francisco de Paula, rodovia RS 20, km 97 (29° 26' 31.1"S, 50° 32' 35,2"W), 20 Nov 2007, *A.A. Schneider 1542* (holotype: ICN; isotypes: K, MO, RB).

Affinis *B. milleflora* sed alis angustioribus, foliis oblongis vel lanceolatis in partis apicalibus ramorum (vs. foliis squamiformibus), alis et foliis granulosis albidis punctiformis differt.

Shrub, 0.8–1.5 m tall; shoots branched, terminating in a capitulescence; **stems** 3-winged, wings to 2–8 mm wide, slightly undulate, distinctly interrupted, grayish green, surface cover with whitish granules (stomata), indument of flagellate hairs. **Leaves** obovate to elliptic, sessile, seemingly 1-veined, covered with whitish granules, indument of flagellate hairs, larger leaves 0.5–1.5 cm long, 0.2–0.6 cm wide, apex obtuse to rounded, base cuneate, margins entire. **Capitula** sessile, in terminal short spikes 1–3 cm long, forming pyramidal panicles. **Male capitula** 3–5 mm long.; flowers 10–17; involucre 2–3 mm long, 2–2.5 wide, campanulate; phyllaries in 3–4 series, outermost phyllaries ovate, median phyllaries lanceolate, innermost phyllaries linear, 2.6–3.1 times as long as the outermost; all phyllaries with margins broadly scarious; apex obtuse fimbriate; corolla 3–4.3 mm long, tube 2–2.5 mm long, lobes 1–1.8 mm long, coiled at maturity; anthers with apical appendage 2.7–3.2 times as long as the filaments, anther apices acute; style slightly exceeding the corolla, with sweeping hairs, the apex nearly fully divided into lanceolate branches, achenes abortive, glabrous and reduced; pappus uniseriate, 3–4 mm long, bristles 15–20, apically broadened and scarcely barbellate. **Female capitula** 5–7 mm long; flowers 20–30; involucre 3–5.5 mm long, 2–3 mm wide, cylindrical; phyllaries in 3–4(–5) series, outermost and median phyllaries like those of male capitula, innermost phyllaries linear, 0.5–0.7 mm long., 0.1–0.2 mm wide; corolla 2.5–3 mm long, 0.1–0.2 mm wide,

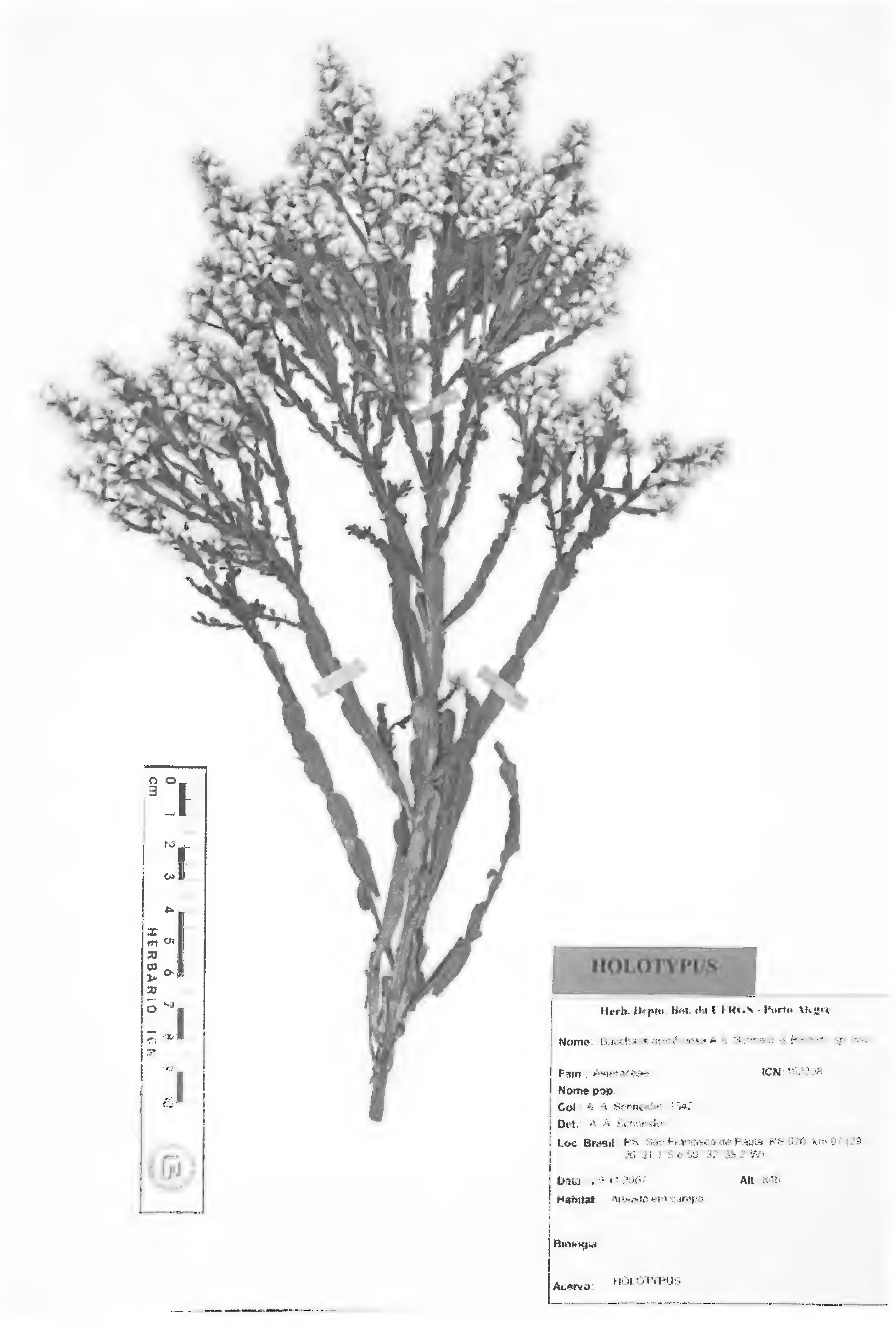

Fig. 1. Holotype of Baccharis apicifoliosa (*A.A. Schneider 1542*, ICN).

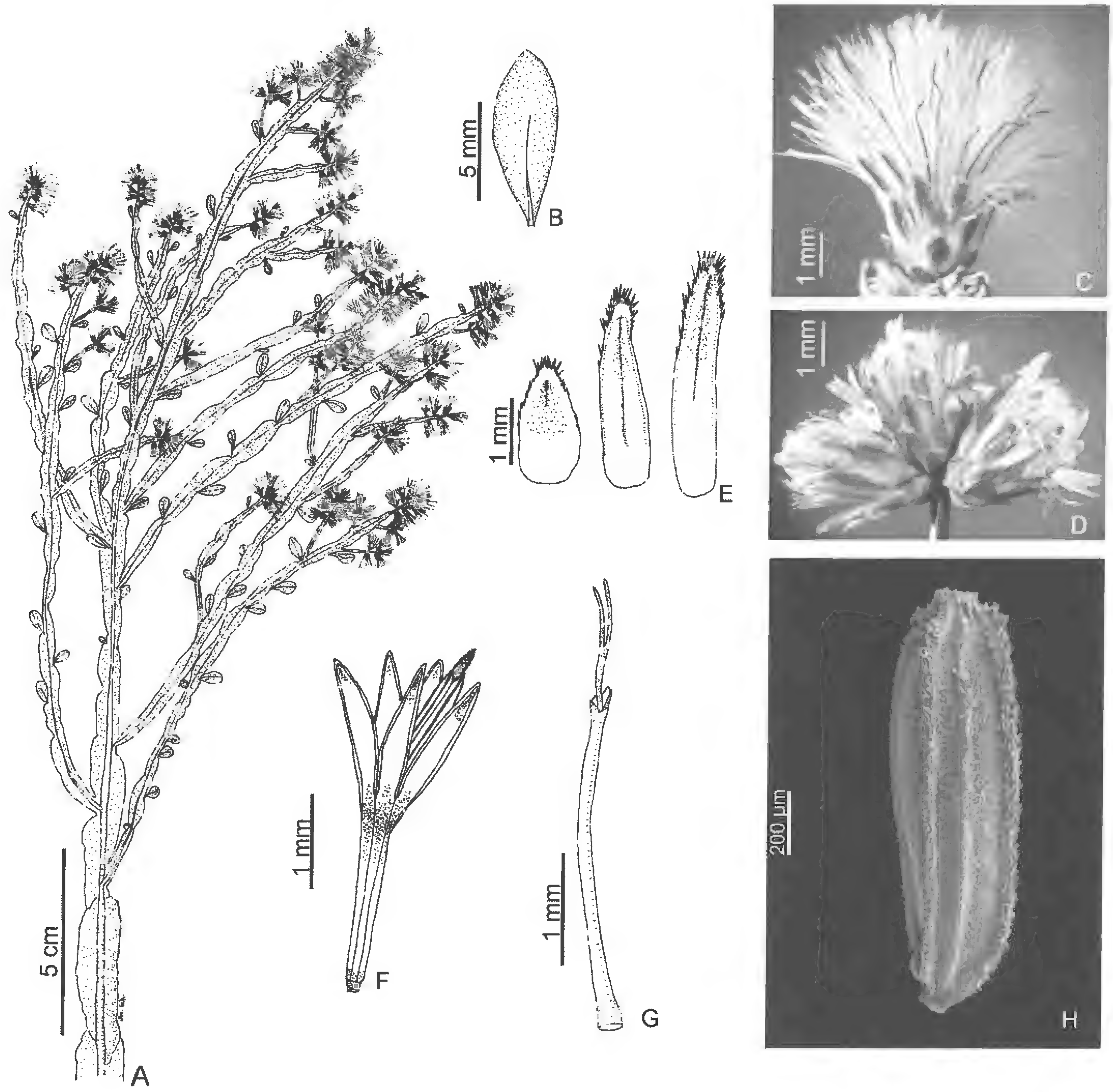

FIG. 2. ***Baccharis apicifoliosa*. A. Flowering branch, female plant. B. Leaf (A and B from *R. Wasum 802* PACA). C. Female capitula. D. Male capitulum. E. Phyllaries of female capitulum (outer to inner). F. Male flower (D and F from *A. Sehnem 5050* PACA). G. Female flower. H. Achene examined by SEM. (C, E, G and H from *A.A. Schneider 1542*, ICN).**

filiform, apex short-ligulate with ligule shallowly 3–5-dentate, glabrous; style 5.2–6.1 mm long, branches 0.4–0.8 mm long; **achenes** 0.9–1.3 mm long, 0.3–0.5 mm wide, nearly cylindric, slightly compressed laterally, covered by low papillae; 5(–7)-ribbed, ribs with papillae more proeminent; **pappus** uniseriate, 3.5–4.5 mm long, bristles 20–25, persistent, basally fused.

Etymology.—The specific epithet refers to the presence of conspicuous leaves only in the apical part of the shoots.

Geographical distribution and habitat.—Restricted to highlands of south Brazil, in the states of Rio Grande do Sul and Santa Catarina. This species grows in grassland, with many individuals occurring abundantly near and in damp areas and often in secondary forests, at altitudes between 750–1500 m, often growing with *B. milleflora*, *B. trimera* (Less.) DC. and *B. articulata* (Lam.) Pers.

PARATYPES. **BRAZIL. Rio Grande do Sul:** Bom Jesus, Fazenda Fundo das Almas, 23 Nov 2001, *R. Wasum 1262* (HUCS, PACA); Cambará

do Sul, Feb 1948, *B. Rambo 36246* (PACA); Montenegro, Linha Pinhal, 20 Nov 1950, *A. Sehnem 5050* (PACA); São Francisco de Paula, rodovia RS 235, 12 Nov 2000, *R. Wasum 726* (HUCS, PACA); estrada para Taquara, 26 Nov 2000, *R. Wasum 773* (HUCS, PACA); Pró-Mata, 1 Oct 2001, *M. Sobral et al. 9394* (ICN). **Santa Catarina:** Bom Retiro, Campo dos Padres, 19 Dec 1948, *R. Reitz 2619* (PACA). Urubici, Serra do Corvo Branco, 17 Oct 2006, *A. A. Schneider 1358* (ICN).

Baccharis apicifoliosa is similar to *Baccharis milleflora* (Less.) DC.; the two species are differentiated by contrasts in the following key.

1. Species with conspicuous leaves, leaves oblong-lanceolate; surface of wings covered with whitish granules; wings to 2–8 mm wide ____ **Baccharis apicifoliosa**
1. Species with squamiform leaves; surface of wings without whitish granules; wings to 5–15(–20) mm wide ____ **Baccharis milleflora**

Baccharis flexuosiramosa A.A. Schneid. & Boldrini, sp. nov. (**Fig. 3–4**). Type: BRAZIL. Rio Grande do Sul: Município de Cambará do Sul, Parque Nacional dos Aparados da Serra, Canyon Itaimbezinho, 7 Dec 2006, *A.A. Schneider 1419* (holotype: ICN; isotypes: K, MO, RB).

Baccharis organensi Baker similis, sed foliis minoribus opacis (vs. vernicosis), ramis alatis (vs. angulatis) flexuosioribus differt.

Shrub, 0.8–2.5 m tall; shoots branched, terminating in a capitulescence; **stems** 3-winged, wings to 2–8 mm wide, plane, attenuate near to the nodes, internodia long, grayish green. **Leaves** oblanceolate-obovate or elliptic, sessile or with a short petiole to 4 mm long, seemingly 1-veined on the adaxial face and 3-veined on the abaxial face, covered with hair tufts, opaque, 1.2–3 cm long, 0.7–1.8 cm wide, apex obtuse to rounded, base attenuate, margins entire, 1-nervate in adaxial face and 3-nervate in abaxial face. **Capitula** sessile, in terminal short spikes, 1–3 cm long, forming pyramidal panicles. **Male capitula** 5 mm long; flowers 20; involucre 4 mm long, 2–2.4 mm wide, campanulate; phyllaries in 3–4 series, outermost phyllaries ovate, median phyllaries broadly lanceolate, innermost phyllaries oblanceolate or lanceolate, 2.8–3.2 times as long as the outermost; all phyllaries with margins broadly scarious; apex acute with fimbriate hairs; corolla 3–3.5 mm long, tube 2–2.5 mm long, with few hairs, lobes 1 mm long, coiled at maturity; anthers with apical appendage 3 times as long as the filaments, apices acute; style slightly exceeding the corolla, with sweeping hairs, the apex nearly fully divided into lanceolate branches, dilated towards apex, with few hairs, achenes abortive glabrous and reduced; pappus uniseriate, 3–3.5 mm long, bristles 15–20, apically broadened and scarcely barbellate. **Female capitula** 5–6 mm long; flowers 20–25; involucre 4.5–5.5 mm long, 2–2.5 mm wide, cylindrical; phyllaries in 3–4 series, outermost and median phyllaries like those of male capitula, innermost phyllaries lanceolate-linear; corolla 2.3–2.6 mm long, 0.1–0.2 mm wide, filiform, ligulate with dentate ligule, glabrous; style 3.1–4 mm long, with few hairs; **achenes** 1.5–1.8 mm long, 0.3–0.5 mm wide, nearly cylindric, slightly compressed laterally, covered with inconspicuous papillae; 6(–8)-ribbed, ribs with papillae more prominent; **pappus** uniseriate, 2.8–3.3 mm long, bristles 15–20, persistent, basally fused.

Etymology.—The specific epithet refers to the flexibility of the shoots.

Geographical distribution and habitat.—Restricted to the highlands of southern Brazil, in the states Rio Grande do Sul and Santa Catarina. This species grows on the borders of cold forests and on shores of rivers at altitudes between 900–1500 m.

Paratypes. **BRAZIL. Rio Grande do Sul:** Município de Cambará do Sul, Parque Nacional dos Aparados da Serra, Canyon Itaimbezinho, 7 Dec 2006, *A.A. Schneider 1420* (ICN); Município de São Francisco de Paula, Distrito de Tainhas, Camping Passo da Ilha, 29° 05' 09.2"S, 50° 21' 48.9"W, 900 m, 4 Dec 2006, *A.A. Schneider 1448* (ICN). **Santa Catarina:** Município de Urubici, Serra do Corvo Branco, 28° 03' 36.5"S , 49° 21' 48.1"W, 1400 m, 18 Oct 2006, *A.A. Schneider 1348*.

Baccharis flexuosiramosa has 3-veined leaves and apparently is closely related to *B. organensis;* the two species differ by contrasts in the following key.

1. Shoots winged; leaves seemingly 1-veined on adaxial face, 1.2–3 cm long, 0.7–1.8 cm wide ____ **Baccharis flexuosiramosa**
1. Shoots not winged; leaves seemingly 3-veined on adaxial face, 3.5–5.5(–6.5) cm long, 1.5–2.6 cm wide wide ____ **Baccharis organensis**

FIG. 3. Holotype of Baccharis flexuosiramosa (*A.A. Schneider 1419*, ICN).

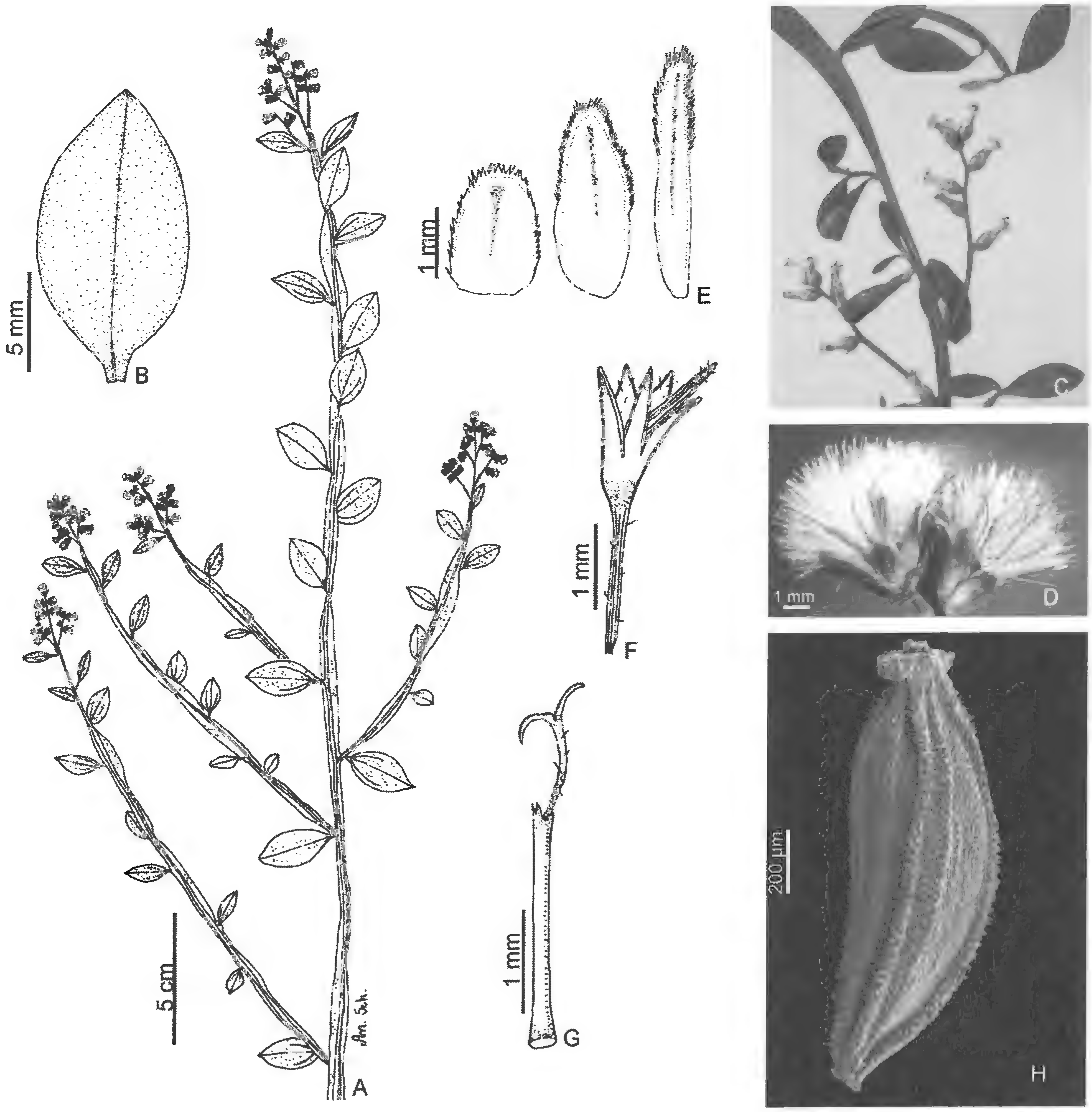

Fig. 4. ***Baccharis flexuosiramosa*****. A. Flowering branch, female plant. B. Leaf. C. Part of female plant with two spikes. D. Female capitula. E. Phyllaries of female capitulum (outer to inner). F. Male flower. G. Female flower. H. Achene examined by SEM (A–C and G–H from *A.A. Schneider 1419,* ICN).**

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BOOK REVIEW

Ian R. Hall, Gordon T. Brown, and Alessandra Zambonelli. 2007. **Taming the Truffle: The History, Lore, and Science of the Ultimate Mushroom.** (ISBN 978-0881928600, hbk.). Timber Press, Inc., 133 S.W. Second Avenue, Suite 450, Portland, Oregon 97204-3527, U.S.A. (**Orders:** www.timberpress.com, mail@timberpress.com, 1-503-227-2878, 1-800-327-5680, 1-503-227-3070 fax). $29.95, 304 pp., 9" × 6".

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4. The Habitats of Some Commercial Truffles.—Périgord Black Truffle; Burgundy or Summer Truffle; Italian White Truffle; Bianchetto; Desert Truffles

This was a delightful book covering most of everything you ever wanted to know about truffles. For instance, I learned that during medieval times, truffles were regarded as witches spit—quite a fall from the 'food of the gods' during the time of Roman rule! Dr. Hall tells us which truffles grow where and describes the flavor of each commercial genus/species of this treasured fungus.

The book is packed with useful information about appropriate growing conditions for specific truffle species, including the proper soil pH and temperature, weather conditions, sun/shade conditions, and trees under which the truffles grow best. Since commercial truffle production is something of the holy grail of expensive crops, this book provides practical information on the care and growing of truffles.

If you are interested in setting up a truffle plantation, this book provides information ranging from soil type to equipment needed to how to train your truffle dog. The authors even caution that truffle pigs may be less likely to give up their found truffle treasure than dogs. If you are just interested in purchasing great truffles for dinner, the authors warn of inferior truffles, tell you when various truffles are in season, and provide at least one French proverb, "Rain in July, truffles for Christmas."

I thoroughly enjoyed this book. It is a lovely luxurious book with many pictures and drawings. That the authors have a wonderful sense of humor is evident in the writing. An extensive appendix lists everything you need to know about truffle production.—*Kay Yount, Tarrant County Master Gardener and BRIT Volunteer, Fort Worth, Texas, U.S.A.*

TWO NEW COTONEASTERS (*COTONEASTER*: ROSACEAE) FROM YUNNAN PROVINCE, CHINA

Jeanette Fryer
Cornhill Cottage, Honeycritch Lane
Froxfield, Petersfield, Hampshire
GU32 1BE ENGLAND

Bertil Hylmö†
Bjuv, SWEDEN

ABSTRACT

Two new cotoneasters are described from Yunnan Province, China. **Cotoneaster qungbixiensis** is distinguished from the similar *C. sternianus* by its thinner, less rugose, deciduous leaves, which are more narrowly elliptic to narrowly ovate. Both species are in the herein described series Sterniani, which differs from series Franchetioides in having semi-evergreen to deciduous foliage that is green not grayish, and paler anther color. **Cotoneaster floridus** of series Dielsiani is separable from *C. dielsianus* by its less shiny and less rugose leaves, fewer-flowered inflorescences, and obovoid fruit.

RESUMEN

Se describen dos nuevos cotoneaster de la provincia de Yunnan, China. **Cotoneaster qungbixiensis** se distingue de *C. sternianus* por sus hojas caducas más delgadas, menos rugosas, que son más estrechamente elípticas a un poco aovadas. Están en la Serie Sterniani descrita como nueva, difiriendo de la Serie Franchetioides en su por tener hojas de semiperennes a caducas que no son verde grisáceas, y el color de las anteras mucho más pálido. **Cotoneaster floridus** de la Serie Dielsiani es separable de *C. dielsianus* por sus hojas menos brillantes y menos rugosas, inflorescencias con menos-flores, y frutos obovoides.

In preparation of a monograph of the genus *Cotoneaster* two new species and one new series have come to light, all in the subgenus *Cotoneaster*, and are described here so the names are available for use in the upcoming treatment of the genus in the Flora of North America.

Cotoneaster series **Sterniani** J. Fryer & B. Hylmö, ser. nov. Type: *Cotoneaster sternianus* (Turrill) Boom, Jaarb. Ned. Dendrol. Ver. 20:81. 1957.

Affinis *Cotoneaster* series Franchetioides Flinck & B. Hylmö sed foliis sempervirens, supra atrovirens, antheris albis, pyrenis 3, –4, –vel 5 differt.

Shrubs, small to medium sized, often densely branched. **Leaves** deciduous or semi-evergreen, subcoriaceous or coriaceous, lower surface tomentose, upper surface rugose. **Inflorescences** 1–20-flowered; the fertile shoots 10–70 mm long. **Flowers** with hypanthium tomentose-pilose. Anthers mostly white. **Fruit** orange-red. Pyrenes (2–)3–4(–5). Fruiting mid to late season.

Cotoneaster series Sterniani includes five species: *Cotoneaster elegans* (Rehder & E.H. Wilson) Flinck & B. Hylmö; *C. induratus* J. Fryer & B. Hylmö; *C. insculptus* Diels; *C. qungbixiensis* J. Fryer & B. Hylmö; and *C. sternianus*. Members of the series Sterniani are distributed in Asia from China (Yunnan, Xizang (Tibet), Sichuan) to Myanmar.

Species belonging to series Sterniani are closely related to those of series Franchetioides, which differ in having evergreen leaves, with the upper leaf surface grayish-green, anthers mauve, pink, or purple, and pyrenes 2 or 3 per fruit.

Cotoneaster qungbixiensis J. Fryer & B. Hylmö, sp. nov. (**Fig. 1**). Type: CHINA. Yunnan: Dali Xian, near Dali, eastern slope of Cangshan, Qung Bi Xi, 15 Sep 1987, *K. Brickell & A. Leslie 12455* (holotype: WSY; isotypes: E, KUN).

Affinis *Cotoneaster sternianus* (Turrill) Boom sed foliis deciduo vel semisempervirens chartaceis in surculorum sterilum angusto-ovatis vel angusto-ellipticis apice acutis vel acutis truncatis et venis 2–4 bini differt.

Shrubs, 2–3 m tall. Branches erect and arched, spreading; branchlets distichous or spiraled, reddish-brown, initially strigose-pilose. **Leaves** deciduous or semi-evergreen, chartaceous, on sterile shoots narrowly ovate or narrowly elliptic, 28–42 × 13–21 mm, base cuneate or obtuse, apex typically acute-truncate, or rarely

Fig. 1. ***Cotoneaster qungbixiensis*****. A.** **Flowering shoot. B, C. Fruiting shoots.**

Fig. 2. ***Cotoneaster floridus*****. A.** **Flowering shoots. B, C. Fruiting shoots.**

acute, lower surface greyish tomentose, upper surface slightly rugose, dark green, shiny, initially pilose, lateral veins 2–4 impressed pairs; petiole 3–4 mm long, often red, strigose-pilose. **Inflorescences** compact, 3–9(–15) flowered; fertile shoots 30–50 mm long with 4–6 leaves; pedicels 1–3 mm, strigose-pilose. **Flowers** (including hypanthium) 7–8 mm long; hypanthium infundibulate, silky tomentose; sepals cuspidate or acuminate, tomentose. Corolla open; petals erect-incurved, pink with dark red base, apex yellowish to off-white. Stamens 20; filaments dark red; anthers white. **Fruit** orange-red, slightly shiny, globose or obovoid, 8–10 mm, pilose, calyx lobes infolded, appressed and forming a flat apex, tomentose. Pyrenes 2–3–4 (ca. 10%–80%–10%), rarely 5, persistent style on abaxial surface, 2/3 from base.

Growing large batches of seeds yields uniform plants, suggesting it is an apomictic tetraploid, like many species of *Cotoneaster* in the subgenus *Cotoneaster* (Hjelmqvist 1962; Bartish et al. 2001) and within other genera of the subfamily Maloidea (Campbell & Dickinson 1990; Campbell et al. 1991). The chromosomes of cultivated material in England were recently counted by both John Bailey and Hugh McAllister, confirming *C. qungbixiensis* is a tetraploid, $2n = 68$.

Other specimens examined: **CHINA. Yunnan:** Dali, E slope of Cangshan Mountain, track to Lonquan Peak, 4 Nov 1996, *J. Fryer JFWY-063* (GB); Yunnan, between Zhongdian and Dali, Beahan Chiang, 22 Sep 1994, *Alpine Garden Society China Expedition 1114* (E); Yunnan, Dali, on Cangshan, above a small temple, Nov 1985, *C. Wingfield 772* (seed accession). **SWEDEN:** Bjuv, cultivated, grown from seed from type collection, Hylmö accession 2087, 11 Jul 1995, *B. Hylmö s.n.* (WTU). **ENGLAND. Hampshire:** Clanfield, cultivated, Rumsey Gardens, seed source *Wingfield 772*, 29 Jun 2001, *J. Fryer 758* (WTU); Hampshire, Sir Harold Hillier Gardens, cultivated, Hillier accession 1994.1175*A, seed source AGS China Expedition No. 2490, 2000, *J. Joyce 293* (HILL), *J. Joyce 13* (HILL). **U.S.A. Washington. King Co.:** Seattle, Washington Park Arboretum, cultivated, accession 189-60-A, 11 Oct 2000, *P.F. Zika 15550* (WTU), same shrub, 24 Jun 2006, *P.F. Zika 22816* (MO, GH, NY, WTU, WTUH); same site, accession 189-60-B, 14 Dec 2006, *P.F. Zika 22901* (WTU, WTUH); same site, accession 162-57-A, 24 Jun 2006, *P.F. Zika 22815* (GH, OSC, WTU, WTUH). **CANADA. British Columbia:** Saanich, Rithets Bog, escaped from cultivation, 20 Jun 2006, *P.F. Zika 22807* (CAN, DAO, GH, NY, UBC, WTU), same site, 21 Oct 2007, *P.F. Zika 23657* (CAN, CAS, DAO, GH, UBC, UC, V, WTU).

Phenology and ecology.—Flowering June to July; fruiting October to November. Natural populations in Yunnan Province, China, are in full sun on rocky slopes over calcareous bedrock. In cultivation, *Cotoneaster qungbixiensis* is hardy to -18°C, and is an attractive shrub with good autumn fruit color.

Cotoneaster qungbixiensis is named for the type locality on Cangshan Mountain in Yunnan. It is closely related to *C. sternianus*, which differs in having leaves that are evergreen, thicker and coriaceous, broadly elliptic to broadly ovate with apex acute or acuminate and lateral veins in 4–6 pairs.

SERIES DIELSIANI G. Klotz, Wiss. Z. Friedrich-Schiller-Univ. Jena, Math.-Naturwiss. Reihe 21:991. 1972.

Cotoneaster floridus J. Fryer & B. Hylmö, sp. nov. (**Fig. 2**). Type: CHINA. Yunnan: Muli, Washin area, near lamasery, 5 Oct 1937, *T.T. Yü 14430* (holotype: E; isotype: A, BM).

Affinis *Cotoneaster dielsianus* E. Pritz. sed foliis chartaceis ad subcoriaceis, supra planities obscurus, inflorescentiis 2–5-floris, fructu oblongo-obovoidus differt.

Shrubs, 1.5–2 m tall. Branches erect and arched; branchlets distichous, maroon and minutely verruculose, initially pilose-strigose. **Leaves** deciduous, chartaceous or subcoriaceous, on sterile shoots elliptic, often broadly so, 15–25 × 11–25 mm, base cuneate or obtuse, apex acuminate or acute, lower surface whitish tomentose-pilose, upper surface dark green, dull, strigose, veins 3(4) slightly impressed pairs; petiole 3–4 mm long, strigose. **Inflorescences** 2–5 flowered; fertile shoots 20–40 mm long, with mostly 4 leaves; pedicels 2–6 mm long, strigose. **Flowers** (including hypanthium) 5–6 mm long. Hypanthium turbinate, densely strigose; sepals cuspidate or acuminate, densely strigose, membranous, reddish-brown, and glabrous near margin, margin villous. Corolla closed; petals erect-incurved, pink with dark red base and white and pink border. Stamens 14–17; filaments dark red or red with pink apex; anthers white. **Fruit** rich red, intensely shiny, narrowly obovoid, 10–11 mm long, sparsely pilose, calyx lobes infolded, appressed, densely pilose. Pyrenes 2–3–4 (ca. 10%–60%–30%), persistent style on abaxial surface, 2/3 from base.

Growing large batches of seed yields uniform plants, suggesting this is another apomictic species, but the chromosomes have not been studied to confirm this.

Other specimens examined: **CHINA. Yunnan:** Chungtien [Zhongdian], Pica, 30 Oct 1937, *T.T. Yü 13905* (A, BM, E). **ENGLAND. Hampshire:** Sir Harold Hillier Gardens, cultivated, Hillier accession 1992.0451*B, 2001, *J. Joyce 329* (HILL).

Cotoneaster floridus is named for its florid red fruits. It is closely related to *C. dielsianus* E. Pritz ex Diels, which differs in its thicker (coriaceous or subcoriaceous) leaves with upper surface slightly rugose and shiny, inflorescences 3–7(–10) flowered, and in its globose fruit.

Phenology and ecology.—Flowering June; fruiting September to October. Little is known about its habitat or associates where it is native in China, in Yunnan and Sichuan Provinces. In cultivation it is hardy to -21°C.

Cotoneaster floridus is frequently found in cultivation as *C. rubens* hort. non W.W. Sm., a misnomer under which it was distributed as seed from the Royal Horticultural Society Wisley Gardens in England. It can also be found under the name *C. dielsianus* var. *rubens* hort. Unfortunately, Professor Yü's collection numbers have become confused in cultivation, hence various species of *Cotoneaster* can sometimes be found under a single collection number.

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MELIOSMA ANTIOQUIENSIS: UNA NUEVA SABIACEAE DE COLOMBIA

Xavier Cornejo

The New York Botanical Garden
200th St. and Kazimiroff Ave.
Bronx, New York 10458-5126 U.S.A.
xcornejo@nybg.org, xcornejoguay@gmail.com

RESUMEN

Se describe una nueva especie arbórea de *Meliosma* (Sabiaceae), del Departamento Antioquia, Colombia. Esta se caracteriza por presentar grandes láminas oblanceoladas, con base atenuada, decurrente, inflorescencias paniculadas con flores pediceladas, laxamente dispuestas en las ramas, pétalos internos muy pequeños, bífidos y estilos muy reducidos o ausentes.

Palabras Clave: Sabiaceae, *Meliosma*, pétalos bífidos, endémica, Colombia

ABSTRACT

A new species of *Meliosma* (Sabiaceae) is described from the Department of Antioquia, Colombia. This is characterized by having large oblanceolate leaf blades with attenuate, decurrent base, paniculate inflorescences bearing pedicellate flowers, that are laxly arranged, very small, bifid inner petals, and very short or absent styles.

Key Words: Sabiaceae, *Meliosma antioquiensis*, bifid petals, endemic, Antioquia, Colombia

INTRODUCCIÓN

Meliosma Blume (Sabiaceae) es un género de árboles y arbustos nativos de Asia y América tropical. En el Neotrópico comprende ca. 70 especies, y se encuentra distribuido desde México hasta Brasil, Bolivia y las Indias Occidentales (Gentry 2001; Morales 2003; Arbeláez 2004; Cornejo, unpubl.). En América del Sur *Meliosma* se encuentra concentrado al norte de los Andes (Gentry 1980, 1986, 1992, 2001; Cornejo 2006), pero el conocimiento taxonómico de muchas de las especies andinas de este género es aún limitado debido a la falta o insuficiencia de especímenes con flores en los herbarios. En la monografía de *Meliosma* para Colombia (Cuatrecasas & Idrobo 1955), se trataron 12 especies, seis de las cuales fueron nuevas para la ciencia. Posteriormente otras seis nuevas especies han sido descritas para la flora de este país (Cuatrecasas & Idrobo 1988; Cuatrecasas 1988; Idrobo 1988). Al revisar el material colombiano, encontré la siguiente novedad.

Meliosma antioquiensis X. Cornejo, sp. nov. (**Figs. 1, 2**). Tipo: COLOMBIA. Antioquia: Mun. Urrao, Parque Nacional Natural Las Orquídeas, margen derecha del Río Calles, en el filo NW de la Cabaña de Calles, bp-PM, Parcela G, subparcela G-13, 06°32'N 76°19'W, 1450 m, 14 Oct 1993 (fl), *A. Cogollo, A. Duque, F. Giraldo, W. Rodríguez & J. Vélez 6887* (holótipo: NY-937622; isótipo: MO-5010854).

Speciei *Meliosma donnellsmithii* Urb. similis, a qua differt folia cum petiolis longioribus (1,5–3,5 cm nec 0,3–1,1 cm), floris pedicellatis (nec sessilis), cum petalis interioribus minoribus (0,7–1 mm nec ca. 1,8 mm), bifidus (nec integro), et stylus absens vel brevissimus (ca. 0,1 mm, nec linearibus, 0,8–1 mm).

Árbol 5 m de alto. Ramas jóvenes densamente estrigosas. Hojas espiraladas; pecíolos 1,5–3,5 cm (incl. pulvínulo 1–1,5 cm) × 4–6 mm, densamente estrigosos; lámina oblanceolada, firmemente cartácea, 40–60 × 15–20 cm, haz café obscuro al secar, ± densamente estrigoso hacia la base del nervio medio, el resto de la lámina glabro, envés café claro al secar, estrigoso a lo largo del nervio medio, el resto de la lámina glabro, con numerosos e inconspicuos puntos glandulares de color rojizo-marrón; ápice ± redondeado, base atenuada, decurrente y obtusa en el extremo basal, margen suavemente repando y remotamente dentado, con inconspicuos y dispersos dientes dispuestos hacia la porción distal de la lámina, nervios secundarios ca. 20–30 pares, fuertemente prominentes en el envés, broquidódromos, nervios terciarios reticulados, prominentes en el envés. Inflorescencia una panícula axilar y subterminal, laxa, ca. 50–65 cm, con ramificaciones hasta

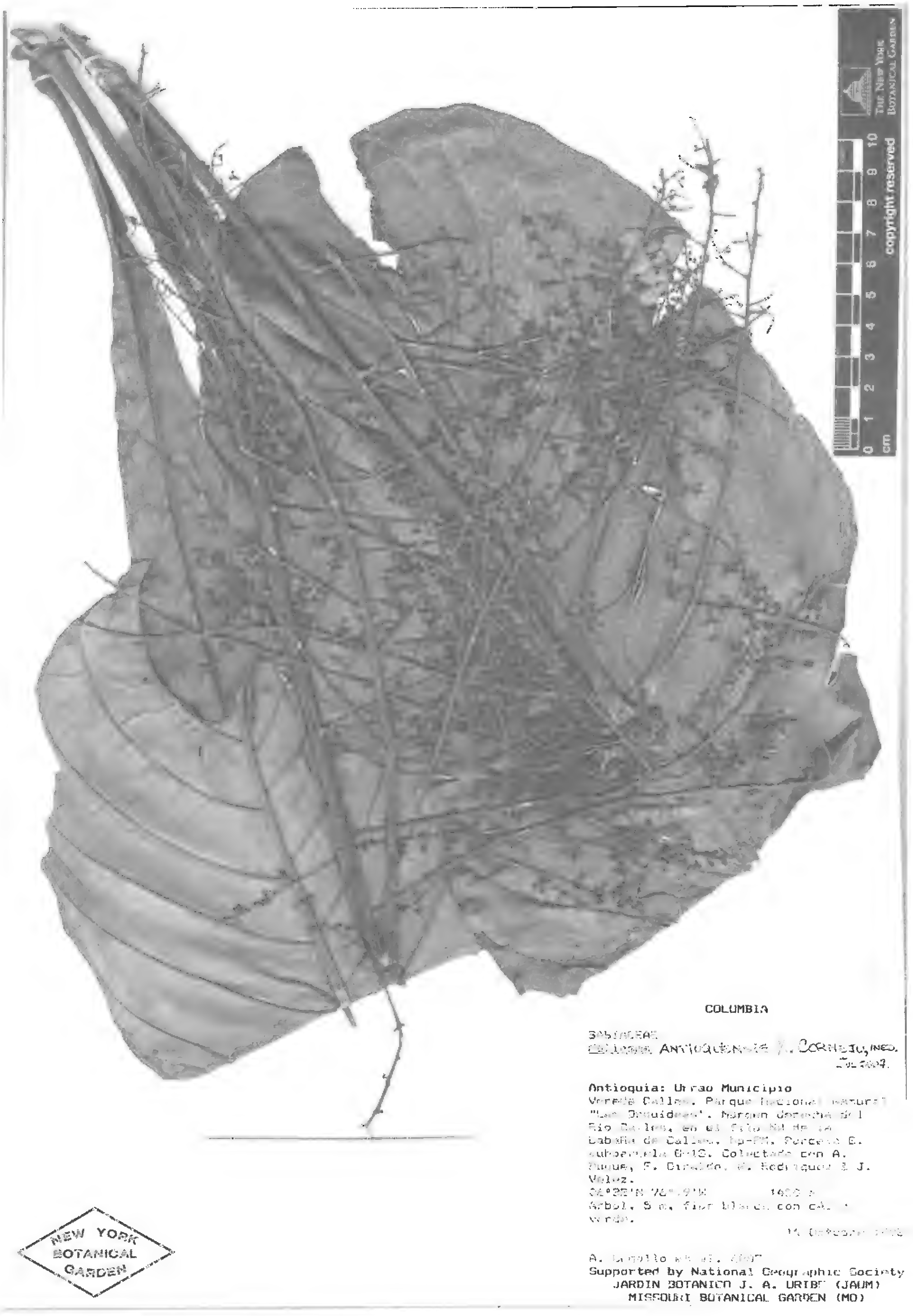

Fig. 1. *Meliosma antioquiensis* X. Cornejo. Fotografía del holótipo, *A. Cogollo et al. 6887* (NY).

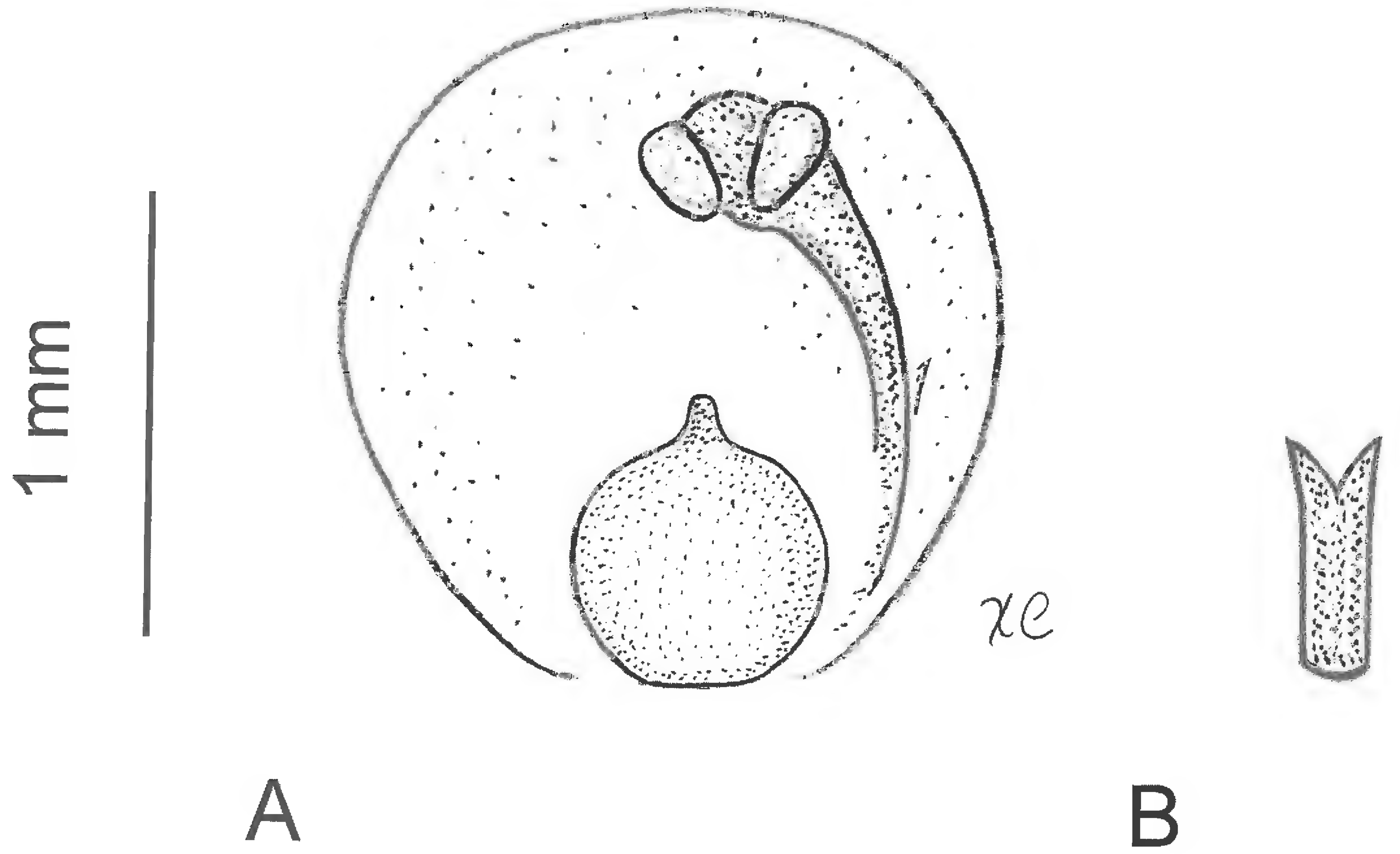

Fig. 2. ***Meliosma antioquiensis*** **X. Cornejo. A. Ovario con muy corto estilo, un estambre y un pétalo externo, en posición hacia la antesis. B. Un pétalo interno. Dibujo del holótipo, *A. Cogollo et al. 6887* (NY).**

de 4 to orden, densamente estrigosa, pedúnculo principal ca. 5 mm diám., ramas secundarias 5–20 cm, las de tercer y cuarto orden con flores pediceladas laxamente dispuestas; brácteas florales ovadas a lanceoladas, 0,6–1,2 × 0,3–0,5 mm, ciliadas; pedicelos 1,5–2,5 mm, mayormente ebracteolados. Sépalos 5, ovados a deltoides o suborbiculares, ca. 0,7–1 × 0,6–1 mm, verdes (en vivo), margen ciliado, el resto glabro. Pétalos externos 3, 1,2–1,8 × 1–2 mm, ± suborbiculares, blancos (en vivo), glabros; pétalos internos 2, oblongoides, 0,7–1 mm, cuya longitud es aproximadamente la mitad de la de los estambres, adnados hacia la base de los filamentos, glabros, bífidos en el ápice. Estambres fértiles 2, 1–1,7 mm. Ovario subgloboso, ca. 0,5 mm, negro al secar, glabro; estilo ausente o muy corto, ca. 0,1 mm, estigma truncado, no diferenciado, con orificio estigmático a veces visible en forma de cruz. Infructescencias glabrescentes, frutos asimétricos obovados, 1,7–2 × 1,3–1,7 cm, 1-quillados, púrpura obscuro al madurar.

Parátipo. **COLOMBIA. Antioquia:** Mun. Urrao, Vereda Calles, Parque Nacional Natural Las Orquídeas, margen derecha del Río Calles, en el filo NW de la Cabaña de Calles, bp-PM, Parcela G, subparcela G-22, 6°32'N 76°19'W, 1450 m, 19 Oct 1993 (fr), *A. Cogollo, A. Duque, F. Giraldo, W. Rodríguez & J. Vélez 7197* (MO).

Etimología.—El epíteto "antioquiensis" se refiere a la localidad del tipo.

Distribución.—Conocida solamente de la localidad del tipo.

Meliosma antioquiensis es una de las especies de este género que posee las hojas más grandes en América del Sur. Vegetativamente es parecida a *M. donnellsmithii*, distribuida en Costa Rica y Nicaragua (Gentry 2001; Morales 2003), pero fácilmente se diferencia de ésta por tener las hojas con los peciolos más largos (1,5–3,5 vs. 0,3–1,1 cm), las flores pediceladas están laxamente dispuestas a lo largo de las ramificaciones (vs. sésiles, densas), los pétalos internos son más pequeños (0,7–1 vs. ca. 1,8 mm), éstos poseen el ápice bífido (vs. entero) y el estilo si presente es muy corto (ca. 0,1 vs. 0,8–1 mm, linear). Por sus flores pediceladas con pétalos internos bífidos, distintivamente más pequeños que los estambres y estilo muy corto, *Meliosma antioquiensis* es parecida a la especie colombiana *M. ellipticifolia* Cuatrec. Sin embargo, esta última difiere por presentar láminas foliares mucho más pequeñas (7–12 × 3,5–5 cm), con menor número de nervios laterales (9–11),

peciolos más cortos (0,6–1 cm), inflorescencia más corta (8–12 cm), y flores con sépalos más grandes (1,5–2 mm). Por sus grandes láminas foliares *Meliosma antioquiensis* es algo similar a *M. itatiaiae* Urb., restringida a las tierras bajas de Brasil, pero ésta presenta hojas con peciolos más cortos (ca. 1 cm), láminas con base redondeada hasta subauriculada y margen fuertemente aserrado, con curvos dientes corniculados e inflorescencias opuestas a las hojas, más densas, que portan flores sésiles.

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ANISOCAPPARIS Y *MONILICARPA*: DOS NUEVOS GÉNEROS DE CAPPARACEAE DE AMÉRICA DEL SUR

Xavier Cornejo
The New York Botanical Garden
200th St. and Kazimiroff Avenue
Bronx, New York 10458-5126, U.S.A.
xcornejo@nybg.org, xcornejoguay@gmail.com
swis@charter.net

Hugh H. Iltis
Department of Botany
University of Wisconsin
430 Lincoln Drive
Madison, Wisconsin 53706, U.S.A.

A. Spencer Tomb
Division of Biology
Kansas State University
Manhattan, Kansas 66506, U.S.A.
astomb@ksu.edu

RESUMEN

Dos nuevos géneros sudamericanos, ambos segregados de *Capparis* L. son descritos e ilustrados: **Anisocapparis** X. Cornejo & H.H. Iltis, éste se caracteriza por presentar flores con cálices anisosépalos, distintivamente decusados-imbricados desde la prefloración, nectarios florales constituidos por cuatro escamas carnosas dimórficas, granos de polen con una ornamentación finamente reticulada y semillas subglobosas fuertemente anisocótilas, con un cotiledón mayor compacto y otro menor muy reducido o ausente. *Anisocapparis* es un género monotípico, distribuido en Bolivia y la parte adyacente del oeste de Brasil, Paraguay y norte de Argentina, y está representado por **Anisocapparis speciosa** (Griseb.) X. Cornejo & H.H. Iltis, comb. nov. El segundo género aquí propuesto es **Monilicarpa** X. Cornejo & H.H. Iltis. Éste se caracteriza por frecuentemente presentar brácteas lineares, hasta de 13 mm en y cerca de la base del pedúnculo de las inflorescencias, flores con cálices gamosépalos que contienen un pequeño hipantio y nectarios florales cupulares o disciformes, en cuyos bordes están fusionados los pétalos, estambres con filamentos insertos en dos verticilos alternos, granos de polen con una ornamentación estriada-reticulada y frutos lineares-torulosos a moniliformes de ápices delgadamente atenuados, que contienen pequeñas semillas elipsoides dispuestas en una hilera, separadas entre sí por las constricciones de las paredes del fruto. *Monilicarpa* comprende dos especies: **Monilicarpa tenuisiliqua** (Jacq.) X. Cornejo & H.H. Iltis, comb. nov., distribuida en el norte de Colombia y Venezuela y **Monilicarpa brasiliana** (Banks ex DC.), X. Cornejo & H.H. Iltis, comb. nov., disyunta al este de Brasil. Se discuten las relaciones de ambos géneros y se provee de una clave para los géneros de Capparaceae de hojas simples, glabros o con pubescencia simple en América.

Palabras Clave: *Anisocapparis, Monilicarpa, Capparis, Capparidastrum*, Capparaceae, new genera, Sudamérica

ABSTRACT

Two new South American genera of Capparaceae, both segregated from *Capparis* L., are described and illustrated herewith: **Anisocapparis** X. Cornejo & H.H. Iltis, characterized by having flowers with anisosepalous calyces, distinctively decussate-imbricate from young bud, floral nectaries of four dimorphic fleshy scales, pollen grains with a fine reticulate surface and strongly anisocotylary subglobose seeds, which have a compact major cotyledon and a very reduced or even totally suppressed minor cotyledon. *Anisocapparis* is a monotypic genus, ranging from Bolivia into adjacent parts of western Brazil, Paraguay and northern Argentina. It is represented by **Anisocapparis speciosa** (Griseb.) X. Cornejo & H.H. Iltis, comb. nov., proposed for a very peculiar species herein transferred from *Capparis* s.l. The second genus herewith proposed is **Monilicarpa** X. Cornejo & H.H. Iltis. This is segregated by virtue of its frequent linear bracts to 13 mm at the base of the inflorescence peduncle, flowers with a gamosepalous calyx that contains a small hypanthium and a cupular or disciform nectary, onto the edges of which the petals are fused into, stamens with filaments inserted in two alternate whorls, pollen grains with a striato-reticulate surface and moniliform or linear-torulose fruits of narrowly-attenuate apex, containing a single row of ellipsoid small seeds, separated by a constriction of the fruit wall. *Monilicarpa* comprises two species: **Monilicarpa tenuisiliqua** (Jacq.) X. Cornejo & H.H. Iltis, comb. nov., from northern Colombia and Venezuela, and **Monilicarpa brasiliana** (Banks ex DC.) X. Cornejo & H.H. Iltis, comb. nov., disjunct to E Brazil. The relationships of both new genera are discussed, and a key to the American genera of Capparaceae with simple leaves, glabrous or with a simple pubescence is also provided.

Key Words: *Anisocapparis, Monilicarpa, Capparis, Capparidastrum*, Capparaceae, new genera, South America

Capparis L. s.s. es un pequeño género de distribución casi estrictamente Holárctica, centrado alrededor de su tipo *Capparis spinosa* L., la especie proveedora de las conocidas *alcaparras* y *alcaparrones* comestibles,

que son los botones florales utilizados como condimento y entremés y los frutos respectivamente (Iltis & Cornejo 2007). Los *Capparis* s.s. son arbustos usualmente procumbentes o pendulares que poseen un par de características espinas retrorsas estipulares, inflorescencias de flores solitarias, zigomorfas, erectas, con el sépalo abaxial galeado (en forma de casco), frecuentemente con pétalos desiguales, androginóforo ausente, estambres en número de 50 hasta numerosos y nectarios florales con el ápice dirigido hacia el interior de la flor (Inocencio et al. 2006). Desde Linneo, la mayoría de las especies americanas de hojas simples de Capparaceae s.s. (excepto *Morisonia* L. y posteriormente *Steriphoma* Spreng.) han sido incluidas y conocidas como *Capparis* s.l., un género extremadamente polimórfico y polifilético, cuyos representantes americanos no corresponden a sus caracteres típicos y cuyo tipo es molecularmente más cercano a *Apophyllum* F. Muell., un género de Capparoideae endémico de Australia, antes que a los *Capparis* del Nuevo Mundo (Hall et al. 2002: 1839; Inocencio et al. 2006: 123). Basado en caracteres morfológicos, Hutchinson (1967: 307) concluyó que más de un género debía de ser reconocido en *Capparis* s.l., y propuso su reordenamiento genérico. Sin embargo, debido a la falta de un conocimiento satisfactorio y a las muy incompletas colecciones de las especies de esta familia en América hace 40 años atrás, el reordenamiento genérico de *Capparis* s.l. propuesto por Hutchinson prácticamente ha sido ignorado.

En años recientes, al realizar los estudios de Capparaceae para Flora Mesoamericana y Flora de Ecuador (Iltis & Cornejo, ms. sometido; Cornejo & Iltis, en prep.), con base a las colecciones neotropicales relativamente más completas obtenidas en las pasadas décadas, así como meticulosas observaciones en campo, ha llegado a ser claro que los *Capparis s.l.* de América son divisibles en varios géneros bien delimitados (Cornejo & Iltis 2006, 2008a, b, c; Iltis & Cornejo 2007, 2008).

En los *Capparis* s.l. de América, el tipo de pubescencia es un caracter muy útil, estable, bien definido y confiable (Iltis et al. 1996). Desde este punto de vista, los *Capparis* s.l. americanos se dividen en dos grandes grupos, que están consistentemente relacionados con el número cromosómico: 1) los de pubescencia simple o glabros, y 2) los de pubescencia peltada a estrellada, candelabra o dendroidea (Iltis & Cornejo, manuscrito sometido). Entre los *Capparis* s.l. de pubescencia simple o glabros están los géneros *Cynophalla* (DC.) J. Presl y *Capparidastrum* Hutch. Las repectivas combinaciones de las especies de estos géneros más un nuevo género Mesoamericano de este grupo están en proceso (Cornejo & Iltis 2008b, c). En esta publicación se presentan dos nuevos géneros sudamericanos pertenecientes al grupo de las Capparaceae de hojas y pubescencias simples.

Para obtener las imágenes de polen se tomaron prefloraciones justo antes de la antesis de los especímenes respectivos (*Vogel 483, de Michel 156, Gentry et al. 10992, Santos et al. 2066, Mori & Kallunki 5379*) que reposan en el herbario WIS y fueron enviadas a la Estación de Agricultura Experimental de Kansas (Kansas Agricultural Experiment Station). Éstas prefloraciones fueron suavizadas en KOH al 10 % y acetolizadas de acuerdo con Erdtman (1960). Las muestras de polen fueron dividas en dos grupos para ser estudiadas en el microscopio de luz (ML) y en el microscopio electrónico de barrido (SEM). Para ML, las muestras de polen fueron montadas en un gel de glicerina y examinadas con un microscopio óptico Zeiss Universal de campo brillante. Para SEM, las muestras de polen fueron suspendidas en agua destilada, pipeteadas sobre un portaobjetos y secadas al ambiente. Las muestras fueron rociadas y recubiertas con una película de oro-paladio y examinadas con un microscopio electrónico Eteck Autoscan SEM, en la Estación de Agricultura Experimental de Kansas. Las placas con los respectivos granos de polen y las imágenes SEM reposan en el herbario WIS de la Universidad de Wisconsin, en Madison.

1. Anisocapparis X. Cornejo & H.H. Iltis, gen. nov. (**Figs. 1, 2, 4**). Typus: *Capparis speciosa* Griseb.

Frutex vel arbores, pubescentia simple vel glabra, folia simple, espiralata, sempervirens, inflorescentia racemosa, terminalia et/vel solitaria et axilaria, floris cum calyx dialisepalis 2-seriatis, decussatis-imbricatis, anisosepalis, nectariae 4-squamae, dimorficae, duo majoribus, duo minoribus, pollen subtiliter reticulatus, fructo pepo subgloboso, indehiscens, cum pericarpio coriaceo, semina sarcotestata in pulpa aurantiaca nidulantia, anisocotila, cotiledon majoribus plerumque subgloboso, compacto et albo.

Árbustos o árboles, glabros o con pubescencia de delicados y frágiles pelos simples. Hojas simples, espiraladas, con peciolos cortos de similar longitud y articulados con las ramas, pulvínulo aparentemente ausente

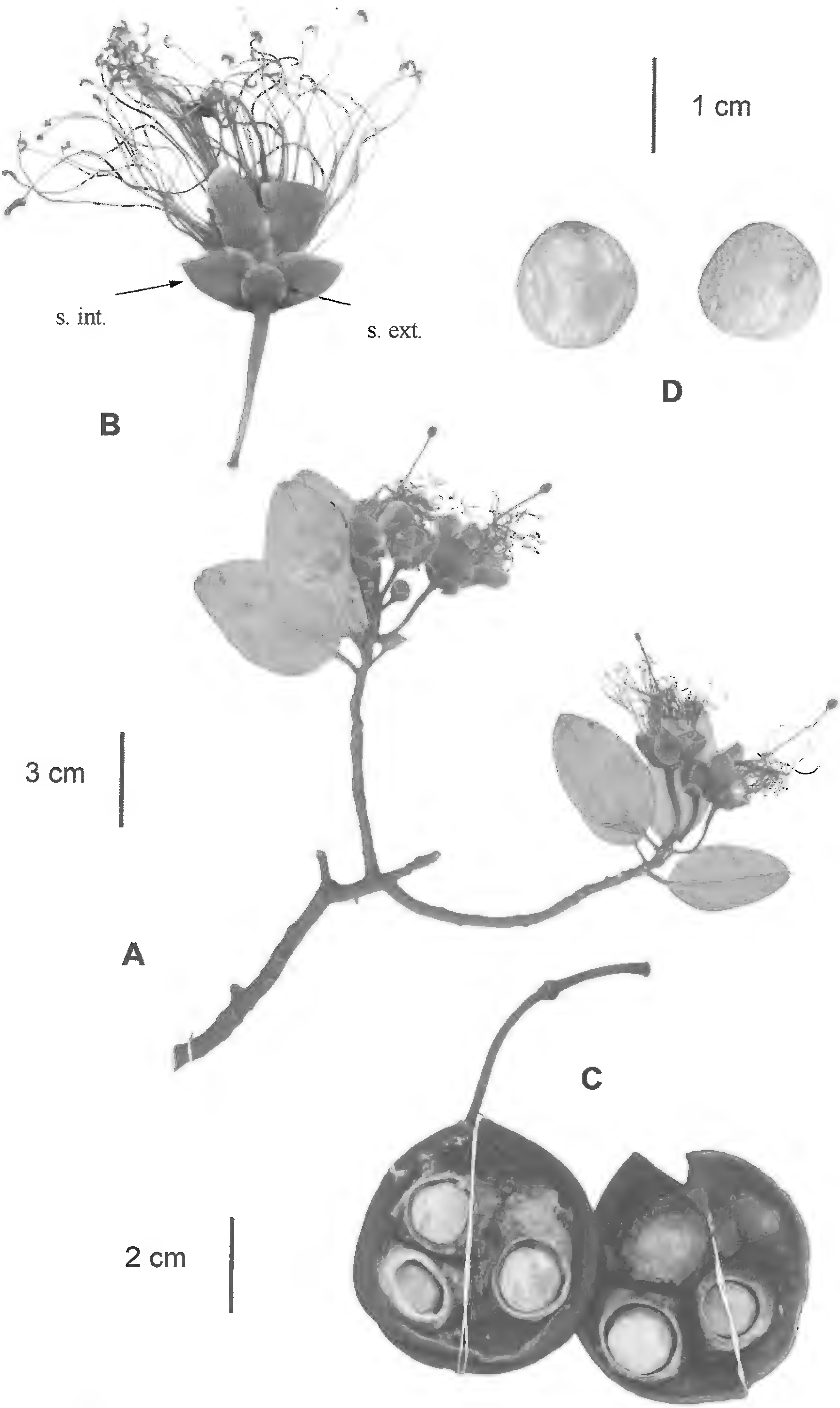


Fig. 1. *Anisocapparis* X. Cornejo & H.H. Iltis: **A.** Rama con inflorescencias terminales (*Nee 46608*, NY). **B.** Flor en antesis, nótese el cáliz anisosépalo, los sépalos externos de distintivo tamaño menor en comparación con los internos, señalados por las flechas (*Nee 51342*, NY). **C.** Frutos cerca de la madurez, y **D.** Corte transversal de las semillas subglobosas, nótese el cotiledón mayor compacto (*Nee & Vargas 44794*, NY).

FIG. 2. *Anisocapparis* X. Cornejo & H.H. Iltis, en vivo: Inflorescencia terminal con varias prefloraciones y una flor en antesis, escala 1 cm. Foto tomada en Bolivia, Dept. Santa Cruz, Prov. Caballero, 64°28'W 17°59.84'S, 1650 m, 8 Ago 2003, cortesía de Michael Nee (NY).

en los especímenes secos. Inflorescencias en racimos terminales, acrópetos y/o flor solitaria y axilar. Cáliz distintivamente 2-seriado, decusado-imbricado y anisosépalo desde las prefloraciones jóvenes, los dos sépalos externos de menos de la mitad del tamaño que los dos sépalos internos. Escamas nectarias cuatro, episépalas, dimórficas, escuamiformes y carnosas, éstas son una proyección de la capa carnosa del tejido nectario que cubre al receptáculo. Las escamas mayores son transversalmente algo oblongas hasta semicirculares, siempre más anchas que altas y varían desde rectas hasta cóncavas y curvadas hacia el receptáculo, a manera de una concha. Corola de aestivación torsiva y/o imbricada, pétalos 4, sésiles, insertos en el receptáculo. Estambres exsertos, ca. 20–50, insertos al mismo nivel sobre un grueso andróforo carnoso (en vivo), éste es plano y a veces algo expandido en el ápice, a manera de un torus (nectarífero?); los estambres internos son glabros, los estambres externos poseen filamentos abundantemente pubescentes en la base, con tricomas unicelulares, ± complanados, ± transparentes; anteras basifijas, granos de polen tricolpados, prolados, con una ornamentación finamente reticulada. Fruto un pepo pendular, globoso o subgloboso, con un pericarpo coriáceo, flexible y con una pulpa de color amarillo hasta anaranjado brillante en la madurez. Semillas uno hasta ocho, con testa dura, subleñosa, cubierta por una sarcotesta de abundantes pelos infiltrados, y embriones fuertemente anisocótilos de cotiledones separados, que poseen un cotiledón mayor compacto, subgloboso, de color blanco marfil y no clorofílico, glabro, y un cotiledón menor muy reducido o ausente (Franceschini & Tressens 2004: 214, fig. 6 [*Capparis speciosa*]).

Anisocapparis es un género monotípico, restringido a Sudamérica en Bolivia, Brasil, Paraguay y Argentina. Éste se caracteriza y distingue de todos los demás géneros americanos (Hutchinson 1967) tradicionalmente tratados en *Capparis* s.l. por presentar: 1) Escamas nectarias dimórficas (vs. nectarios [e.g., *Cynophalla*], escamas nectarias [*Beautempsia*] o apéndices nectarios [e.g., *Capparicordis*], siempre isomórficos); 2) semillas ± subglobosas (vs. cocleadas o reniformes hasta elípticas); y, 3) embriones con cotiledones separados,

extremadamente anisocótilos, muy distintos en tamaño y forma entre sí, con un cotiledón mayor compacto, especializado para almacenar (Fig. 1D), y un cotiledón menor muy reducido o ausente, único en las Capparaceae del Nuevo Mundo. Éstos han sido discutidos en detalle e ilustrados por Franceschini & Tressens (2004 [ver *Capparis speciosa*]).

Por la apariencia externa de sus frutos y el color blanco marfil de los embriones de sus semillas, *Anisocapparis* superficialmente se asemeja a algunos miembros de *Capparidastrum* Hutch. (e.g., *Caparidastrum petiolaris* [Kunth] Hutch., comparar con Cornejo & Iltis 2005a: 158, fig. 2C [tratado como *Capparis petiolaris*]). Pero además de los tres caracteres anteriormente mencionados, *Anisocapparis* también se diferencia de *Capparidastrum* por tener un cáliz notoriamente anisosépalo, con aestivación decusada-imbricada (vs. cáliz isosépalo, frecuentemente 1-seriado) y granos de polen con una ornamentación finamente reticulada (Fig. 4, vs. tectada-espinulosa [Fig. 7] o tectada-perforada). Otras diferencias menores de *Anisocapparis* en comparación con *Capparidastrum* son la presencia de láminas foliares de menores dimensiones, 3–8 cm (vs. usualmente 10–50 cm), y una densa pubescencia en la base de los filamentos de los estambres externos (vs. filamentos glabros), cuya función es desconocida. Bajo el estereoscopio se ha observado que ésta retiene granos de polen, por lo que se presume podría estar relacionada con la polinización.

Entre las Capparaceae de América, el tipo de cáliz anisosépalo que presenta *Anisocapparis*, con los sépalos dimórficos dispuestos en dos series, decusados-imbricados desde la prefloración, cuyo par de sépalos suborbiculares externos es de menor dimensión en comparación con el par de sépalos internos, es solamente similar a *Cynophalla* (Iltis & Cornejo 2005, tratado como *Capparis* subg. *Cynophalla*). Debido a esta similitud, la especie tipo de *Anisocapparis* (*Capparis speciosa*) fue originalmente descrita como perteneciente a las "Cynophalla" (Grisebach 1879: 18). Pero *Anisocapparis* fácilmente se diferencia de *Cynophalla* por la ausencia de las características glándulas nectarias extraflorales, dispuestas en las axilas de las ramas terminales e inflorescencias; también por la diferente estructura y disposición de los nectarios florales (éstos en *Cynophalla* son siempre isomórficos, planos hasta un poco cóncavos y dispuestos ± horizontalmente sobre el receptáculo), y por el polen de escultura finamente reticulada (vs. tectado-espinuloso en *Cynophalla*). Además, los pepos globosos a subglobosos, con semillas subglobosas, anisocótilas, de cotiledones separados con un cotiledón mayor muy desarrollado y compacto, especializado para almacenar, de color blanco y no clorofílico de *Anisocapparis*, contrasta grandemente con los frutos capsulares, dehiscentes, con semillas elipsoideas, isocótilas, de embriones de cotiledones delgados, convolutos, verdes y clorofílicos de *Cynophalla* (véase en Franceschini & Tressens 2004 [*Capparis speciosa* vs. *C. flexuosa* L. y *C. retusa*]; Iltis & Cornejo 2005).

Etimología.—*Aniso*, el prefijo de su nombre, se refiere a los distintos tamaños de los sépalos, nectarios florales y cotiledones que caracterizan a este nuevo género.

Anisocapparis speciosa (Griseb.) X. Cornejo & H.H. Iltis, comb. nov. Basónimo: *Capparis speciosa* Griseb., Abh. Königl. Ges. Wiss. Göttingen 24:18. 1879. Non *Capparis speciosa* Moric., *nomen nudum* escrito en *Blanchet 2564* (NY!), citado en Eichler in Martius, Flora Brasiliensis 13:272. 1865 (= *Colicodendron yco* Martius). Non *Capparis speciosa* Miranda, Anal. Inst. Biol. Mex. 24:77. 1953, *nom. illeg.* (= *Capparis mollicella* Standley). *Capparis speciosa* Griseb. var. *normalis* Kuntze, Rev. Gen. Pl. 3:7. 1898. Tipo: ARGENTINA. Gran Chaco: Prov. Salta, Dept. Orán, prope Dragones (Fuerte Sarmiento), 13–18 Ago 1873 (fl), "Naranjillo," *P.G. Lorentz & G. Hieronymus 601* (lectótipo: GOET!, designado en Gómez 1953: 298; isótipos: B-10 0242734!, K-220554!, NY-967902! [herb. O. Kuntze]).

Capparis pruinosa Griseb., Abh. Königl. Ges. Wiss. Göttingen 24:19. 1879. *Capparis speciosa* var. *pruinosa* Hassler, Repert. Spec. Nov. Regni Veg. 12:254. 1913. Tipo: ARGENTINA. Prov. Salta: San Lorenzo, entre Pampa Blanca y Santa Rosa, Nov 1873, *P. G. Lorentz & G. Hieronymus 227* (lectótipo, aquí designado: GOET!).

Capparis speciosa Griseb. var. *ovata* Kuntze, Rev. Gen. Pl. 3:7. 1898. Tipo: BOLIVIA: Sierra de Santa Cruz, 2000 m, sin fecha, *O. Kuntze s.n.* (LECTÓTIPO, aquí designado: NY 581261! [herb.O. Kuntze]).

Capparis speciosa Griseb. var. *lanceolata* Kuntze, Rev. Gen. Pl. 3:7. 1898. Tipo: BRASIL. Mattogrosso, Corumba, Jul 1892 (fl), *O. Kuntze s.n.* (LECTÓTIPO, aquí designado: B 10 0242735! [foto en WIS!]).

Capparis malmeana Gilg, Engl. Bot. Jahrb. 25 Beibl. 60:23. 1898. *Capparis speciosa* var. *pruinosa* f. *malmeana* (Gilg) Hassler, Repert. Spec. Nov. Regni Veg. 12:254. 1913. Tipo: PARAGUAY: "Colonia Risso pr. Rio Apao. In silva regionis calcarea," 26 Sep 1893 (fl), *G. Malme 1000* (lectótipo, aquí designado: B 10 0242733! [F foto neg. 5807 en NY!, WIS!]; isótipo: S).

En la publicación original de *Capparis speciosa*, Griseb. solamente mencionó que esta especie estaba basada en

una colección de Lorentz & Hieronymus proveniente de Dragones, donde floreció en Agosto. En el herbario GOET, el lectótipo *Lorentz & G. Hieronymus 601*, es la única colección identificada como "*Capparis speciosa* Gr. n. sp.," proveniente de Dragones y colectada con flores en Agosto.

Capparis speciosa var. *normalis* fue propuesta con base a un duplicado del mismo tipo de *Capparis speciosa* (*Lorentz & G. Hieronymus 601*) que reposaba en el herbario de Kuntze, actualmente en NY. Este duplicado fue identificado por Kuntze en letra manuscrita como "*Capparis speciosa* Gris. α *normalis* foliis oblongis." Esta leyenda concuerda con "folia oblonga," el carácter propuesto para esta variedad en su publicación original por lo que no hay duda de que la var. *normalis* de Kuntze fue basada en el mismo tipo de *Capparis speciosa*.

En el herbario GOET hay dos colecciones identificadas como *Capparis pruinosa* y marcadas como tipos, *Lorentz & Hieronymus 227*, con fecha Nov 1873 y *Lorentz & Hieronymus 1182*, con fecha 7 Dic 1873. En la publicación original de *Capparis pruinosa* Grisebach no mencionó colección tipo alguna, solamente "ubi floret Novembri." *Lorentz & Hieronymus 227* está escrita a mano "*Capparis pruinosa* Gr. n sp," y su fecha de colección concuerda con la fecha referida en la publicación original, por tanto esta última colección es aquí designada lectótipo. En K, la colección K-220553 tiene dos etiquetas que leen "*Capparis pruinosa* Gr. Salta" y "Argentine Comm. Dr. Grisebach, Dec. 1878." Aunque esa es una colección histórica, sin embargo carece de mayor información y no se puede determinar si es un duplicado del lectótipo.

Nombres locales.—ARGENTINA: Meloncillo (*Venturi 9807*), naranjo del monte (Gómez 1953), naranjillo (Grisebach 1879, public. orig.), payaguá-naranja, sacha limón (*Ruiz et al. 10540*), sacha naranja, sacha sandía (Gómez 1953). BOLIVIA: Alcaparro (*Nee & Coimbra 35565*), coca de chivo (*Nee 51204*). PARAGUAY: Bola verde (*Spichiger & P. Loizeau 1519*); i'tsá'jituk [pl: i'tsájituki], 'tso'xuá'nuk [pl: 'tso'xuá'nki] (*T. Gragson 153*, Manxuj); Pachyajua naranja (*Spichiger & Loizeau 1504*).

Usos.—Los frutos de *Anisocapparis speciosa* al madurar caen al suelo y la pulpa en el interior se vuelve muy suave, de color naranja brillante. Éstos se parten a lo largo de las suturas al presionarlos con los dedos, la pulpa es consumida directamente y la piel es desechada. La consistencia de los frutos es como la de los mangos (*Mangifera indica* L.), y tienen un sabor agridulce, entre mango y naranja (*T. Gragson 153*). *Anisocapparis speciosa* es principalmente utilizada para forraje. El ganado come las hojas y frutos de esta especie durante todo el año, aunque está reportado que las vacas se atoran al intentar tragar el fruto (Vargas et al. 2000).

Fenología.—Floración nocturna (*Vogel 483*).

Interacciones biológicas.—Las flores de *Anisocapparis speciosa* son visitadas por por abejas melíferas y grandes avispas negras (Vargas et al. 2000, *Nee 51204*). Sus frutos son alimento de mamíferos, como los venados *Mazama americana* y *M. goauzoubira* (Stallings 1984; Rivero et al. 2005). Así como en otras especies de Capparaceae de frutos grandes en América (Iltis et al. 1996), se presume que los frutos de *Anisocapparis speciosa* en el pasado sirvieron de alimento para una megafauna extinta en la actualidad.

Especímenes representativos. **ARGENTINA. Prov. Corrientes:** Dept. Capital, by the road side ca. 1 km S of Paso Lessoa, 22 Ago 1951 (fl), *T.M. Pedersen 1147* (NY). **Prov. Salta:** Dept. General Güemes, 5 km NW de Fuerte Esperanza por la ruta Juana Azurduy (ruta Prov. 52), 25°08'S 61°52'W, 13 Dic 1999 (fl), *R. Fortunato, A. D'Agostini, A. Martínez & H. López 6391* (MO, NY); Pasando Güemes, en el km 1440 de la ruta, 34 m, 20 Nov 1974 (fl), *V. Ruiz, R. Roncalia & A. Cuezzo 10540* (NY). **Dept. Guachipas:** Alemanía, 1300 m, 4 Nov 1929 (fl), *S. Venturi 9807* (MO, NY). **Dept. Orán:** Dragones, Ruta Nac. 81, beside railway line, 20 Nov 1978 (fl, fr), *S. Renvoize 3543* (MO, NY). **Prov. Santiago del Estero:** Dept. Choya, 12 km W de Villa la Punta en dirección a Frías, 28°23'S 64°46'W, 257 m, 30 Nov 1995 (fl), *R. Fortunato & Micheli 5153* (NY, US). **BOLIVIA. Dept. Chuquisaca:** Prov. Luis Calvo, Estancia Acapulco, 300 m, 20°20'S 06°15'W, 3 Ene 1995 (fl), *L. Sánchez 55* (USZ, ex Tropicos). **Dept. Cochabamba:** Puente Arce, 1800 m, 18°35'S 65°10'W, 11 Apr 1963, *D. Ugent & M. Cárdenas 4884* (US, WIS); Prov. Narciso Campero, Aiquile, 34 km hacia Epizana, 1770 m, 17 Oct 1984 (fl, fr), *S.G. Beck 8922* (NY, WIS). **Dept. Santa Cruz:** Prov. Andrés Ibáñez, at quebrada, 10.5 km SSE of center of Cotoca, 9.5 km SSE of turnoff from highway bypass at Cotoca on dirt road to Paurito, 17°50'S 62°57'30"W, 345 m, 5 Ene 1996 (fr), *M. Nee 46704* (MO, NY); Prov. Caballero: Comarapa 5 km hacia Santa Cruz, 1950 m, 28 Sep 1981 (fl), *S.G. Beck 7070* (NY, WIS); 11 km (by air) SW of Comarapa on road to Chilón, 17°59'S 64°35'W, 1600 m, 7 Ago 1987 (fl), *M. Nee & G. Coimbra 35565* (MO, NY); 5.5 km N of center of Saipina on dirt road to Chilón, valley of Río Comarapa, 18°03'27"S 64°36'13"W, 1405 m, 8 Dic 2005 (fl), *M. Nee, D. Villaroel & O. Colque 53664* (NY). 0.5 km SE of turnoff (to Pulquina), on SE side of Palizada along hwy from San Isidro to Mataral and Mairana, 18°03'3"S 64°25'30"W, 1575 m, 29 Dic 1995 (fl), *M. Nee 46608* (NY). Strauch der Kakteensteppe im Trockental bei Comarapa, unweit San Isidro, centrale Ostkordillere Boliviens, Blüten nocturn, gelbgrün bis hellgrün, Filamente weiss, starr, 1800 m, 13 Ene 1965 (fl), *S. Vogel 483* (A, F, WIS, Z). **Prov. Chiquitos:** Pozo del Tigre, 135 km E de la ciudad de Santa Cruz, propiedad de la empresa ABAFA, alrededores campamento principal, 17°34'S 61°57'W, ca.

250 m, 28 Dic 1994 (fr), *S. Ortiz & G. Castro 106* (NY, USZ). **Prov. Cordillera,** 1 km N of YPFB Planta de Gas at the Río Grande, 18°10'S 62°54'W, 350 m, 3 Dic 1989 (fl, fr), *M. Nee 37899* (MO, NY, WIS); 1.2 km E of Camiri-Ipatí road, on dirt road toward Eití, 19°54.39'S 63°31.59'W, 950 m, 8 Nov 2000 (fl, fr j.), *M. Nee 51302* (MO, NY); along road from Ipatí to Abapó, 17 km NNE of Ipatí, 19°38'S 63°33'W, 980 m, 10 Nov 2000 (fl) *M. Nee 51342* (MO, NY); 2.5 km E of Comunidad Salinas from turnoff of the Camiri-Cuevo hwy, 20°13'S 63°26'W, 880 m, 6 Nov 2000 (fl), *M. Nee 51204* (MO, NY); Alto Parapetí, bosque natural, en depresion de ladera, 850 m, 8 Ene1982 (fl, fr), *R. de Michel 156* (WIS). **Prov. Florida:** 5 km al S de Mataral on road to Vallegrande, 18°09'S 64°13'W, 1400 m, 15 Dic 1990 (fr), *M. Nee 40285* (NY, USZ). 7 km (by air), 10.2 km (by road) NNW of Mataral on road to San Juan del Potrero, 18° 02'45"S 64°14'25"W, 1475 m, 30 Ene 1994 (fr), *M. Nee & I. Vargas 44794* (MO, NY, WIS). **PARAGUAY. Dept. Boquerón:** Mariscal Estigarribia, 22°01'49"S 60°36'52"W, 250 m, 15 Dic 1998 (fl, y fr), *E. Zardini & L. Guerrero 49966* (MO, NY); Estancia Copel, 22°12'S 61°54'W, 150 m, 19 Sep 1985 (fl), *R. Spichiger & P. Loizeau 1519* (MO, NY). **Dept. Presidente Hayes:** Estancia Pozo Favorito, 59°53'W 23°7'S, 150 m, 19 Sep 1985 (fl), *R. Spichiger & P. Loizeau 1504* (MO, NY); 8 km before 25 Leguas, Trans Chaco hwy SE of Filadelfia, 22°45'S 59°45'W, ca. 200 m, 2 Oct 1985 (fl), *A. Gentry, L. Pérez & D. Brunner 52003* (MO, NY); Chaco, vic. Manxuj, 21°48'S 61°41'W, 15 Jul 1993, *T. Gragson 153* (MO).

2. Monilicarpa X. Cornejo & H.H. Iltis, gen. nov. (**Figs. 3, 5, 6**). TYPUS: *Capparis tenuisiliqua* Jacq.

Frutex vel arbores, pubescentia simple vel glabra, folia simple, spiralata, subopposita vel 3-subverticillata, decidua vel sempervirens, inflorescentia racemosa, terminalia, floris cum calyx gamosepalis 1-seriatis, sepalis aequalis, erectis, petalis in nectariis cupularibus vel disciformibus insertiis, pollen striato-reticulato, fructus capsularis linearibus-torulosibus vel moniliformibus, dehiscentibus, cum semina elipsoidea, 1-linearia disposita, embryo convoluto.

Subarbustos, arbustos o arbolillos, mono a multicaules, con pubescencia de pelos simples o glabros. Hojas simples, espiraladas y con peciolos de similar longitud o subopuestas y 3-subverticiladas y subsésiles, pulvínulo presente o ausente. Inflorescencias en racimos terminales, acrópetos; frecuentemente con brácteas lineares, hasta 13 mm, localizadas en- y cerca de- la base del pedúnculo de la inflorescencia. Cáliz gamosépalo, 1-seriado, sépalos 4, isomórficos, triangulares, en la antesis erectos y fusionados hacia la base, provisto al interior de un pequeño hipantio que contiene un nectario floral cupular o disciforme de bordes libres o fusionado con el hipantio, con o sin 4 apéndices alternipétalos. Corola de aestivación siniestrorsa-torsiva, pétalos 4, fusionados en el borde superior del nectario. Estambres exsertos, ca. 15 a 30, glabros, insertos en dos verticilos alternos sobre un corto y apenas expandido andróforo, anteras basifijas, granos de polen tricolpados, prolados, con una ornamentación estriada-reticulada. Frutos cápsulas lineares-torulosas a moniliformes, con ápice delgado-atenuado, dehiscentes o tardíamente dehiscentes, esencialmente sin pulpa, con 1 hasta 22(–32 [según Ruiz-Zapata 2002: 150]) semillas elipsoides dispuestas en una hilera, testa presente, embrión verde o aparentemente crema, convoluto.

Monilicarpa se caracteriza por frecuentemente presentar brácteas lineares, hasta de 13 mm, localizadas en y cerca de la base del pedúnculo de las inflorescencias, flores con cálices gamosépalos que contienen un pequeño hipantio, nectarios florales cupulares o disciformes, en cuyos bordes están fusionados los pétalos, filamentos de los estambres insertos en dos verticilos alternos, granos de polen poseen una ornamentación estriada-reticulada (Figs. 5, 6, única entre los seis tipos de polen observados entre las Capparaceae de hojas simples en el Neotrópico), y frutos lineares-torulosos a moniliformes, de ápices delgadamente atenuados, que contienen pequeñas semillas elipsoides dispuestas en una hilera, separadas entre sí por las constricciones de las paredes del fruto.

El nectario floral cupular o disciforme de *Monilicarpa* está localizado alrededor de un androginóforo central y fusionado al interior de- y recubriendo a- un pequeño e inconspicuo hipantio. Debido a la presencia de este pequeño hipantio, el cáliz de *Capparis viridiflora* Kunth (Humboldt et al. 1821: 92), uno de los sinónimos aquí citados de *Monilicarpa tenuisiliqua*, originalmente fue descrito como: "turbinato-urceolatus." El nectario floral de *Monilicarpa* en sus bordes y entre las bases de los pétalos posee cuatro apéndices erectos, dentados o triangulares (*Monilicarpa tenuisiliqua*) o rudimentarios en forma de inconspicuos lóbulos o ausentes (*M. brasiliana*), como se aprecia en la lámina de *Capparis brasiliana* en Flora Brasiliensis (Eichler en Martius 1865: 279, tab. 62, fig. 1:3, nótese el borde superior libre y separado del cáliz). En contraste, *Capparidastrum* y *Cynophalla*, los géneros restantes de las Capparaceae de hojas y pubescencias simples en América, tienen flores con cuatro nectarios, apéndices o escamas nectarias y pétalos insertos sobre un receptáculo usualmente plano. Adicionalmente, *Monilicarpa* se diferencia de *Capparidastrum* por tener los filamentos de los estambres insertos en dos verticilos (vs. filamentos de los estambres insertos en varios verticilos), y los

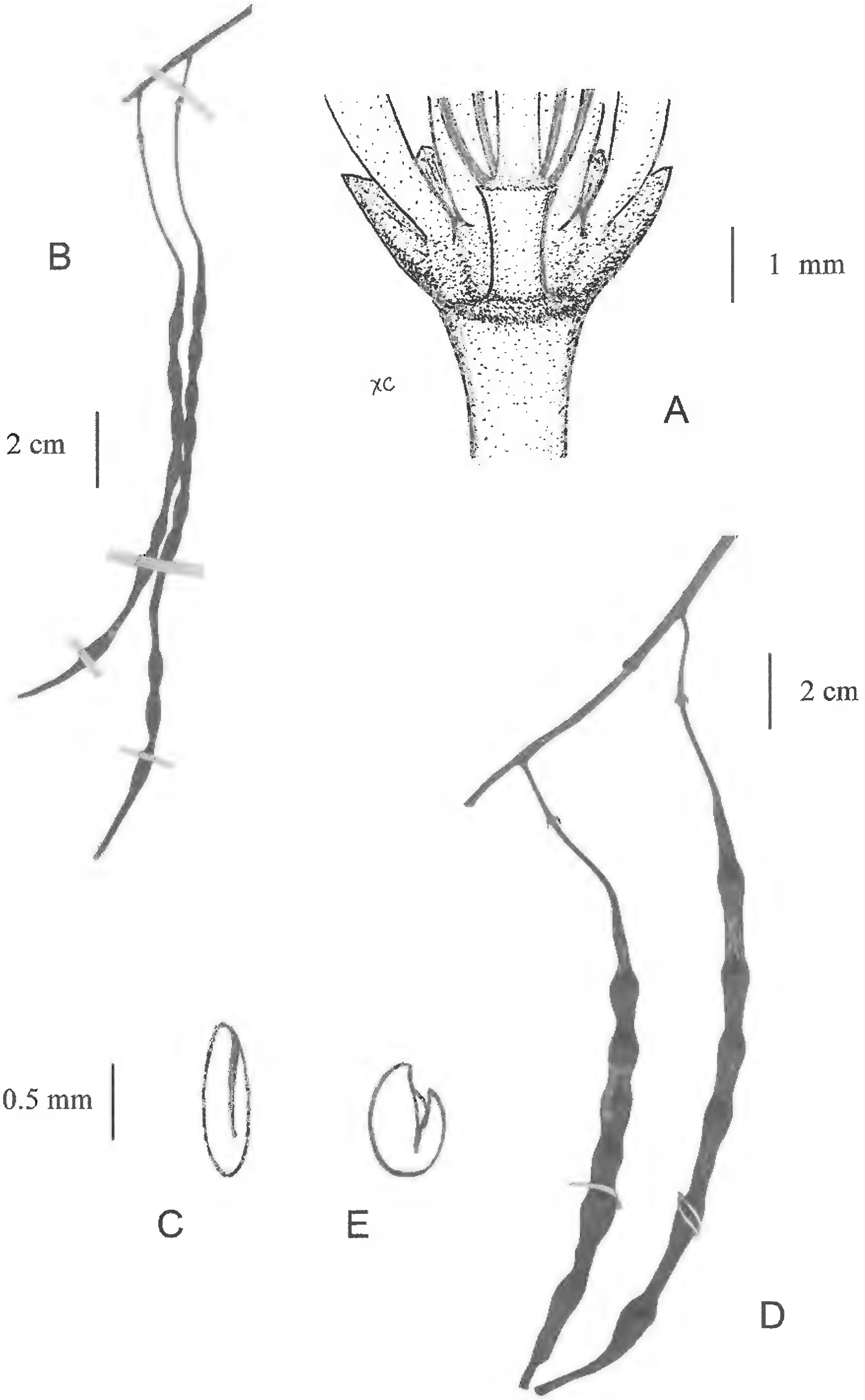


Fig. 3. *Monilicarpa* X. Cornejo & H.H. Iltis: *Monilicarpa tenuisiliqua* (Jacq.) X. Cornejo & H.H. Iltis. **A.** Diagrama de un cáliz con el pétalo frontal removido, nótese los pétalos fusionados sobre el borde de un nectario cupular que recubre al hipantio y no insertos en el receptáculo (*Ruiz & Rondón 3641*, NY). **B.** Parte de una infructescencia con dos frutos cuyas semillas están dispuestas en una hilera (*Smith 843*, NY). **C.** Diagrama de un embrión (*Bunting 5400*, WIS). *Monilicarpa brasiliana* (Banks ex DC.) X. Cornejo & H.H. Iltis. **D.** Parte de una infructescencia con dos frutos cuyas semillas están dispuestas en una hilera (*Duarte 6422*, NY). **E.** Diagrama de un embrión (*Araujo 3857*, WIS).

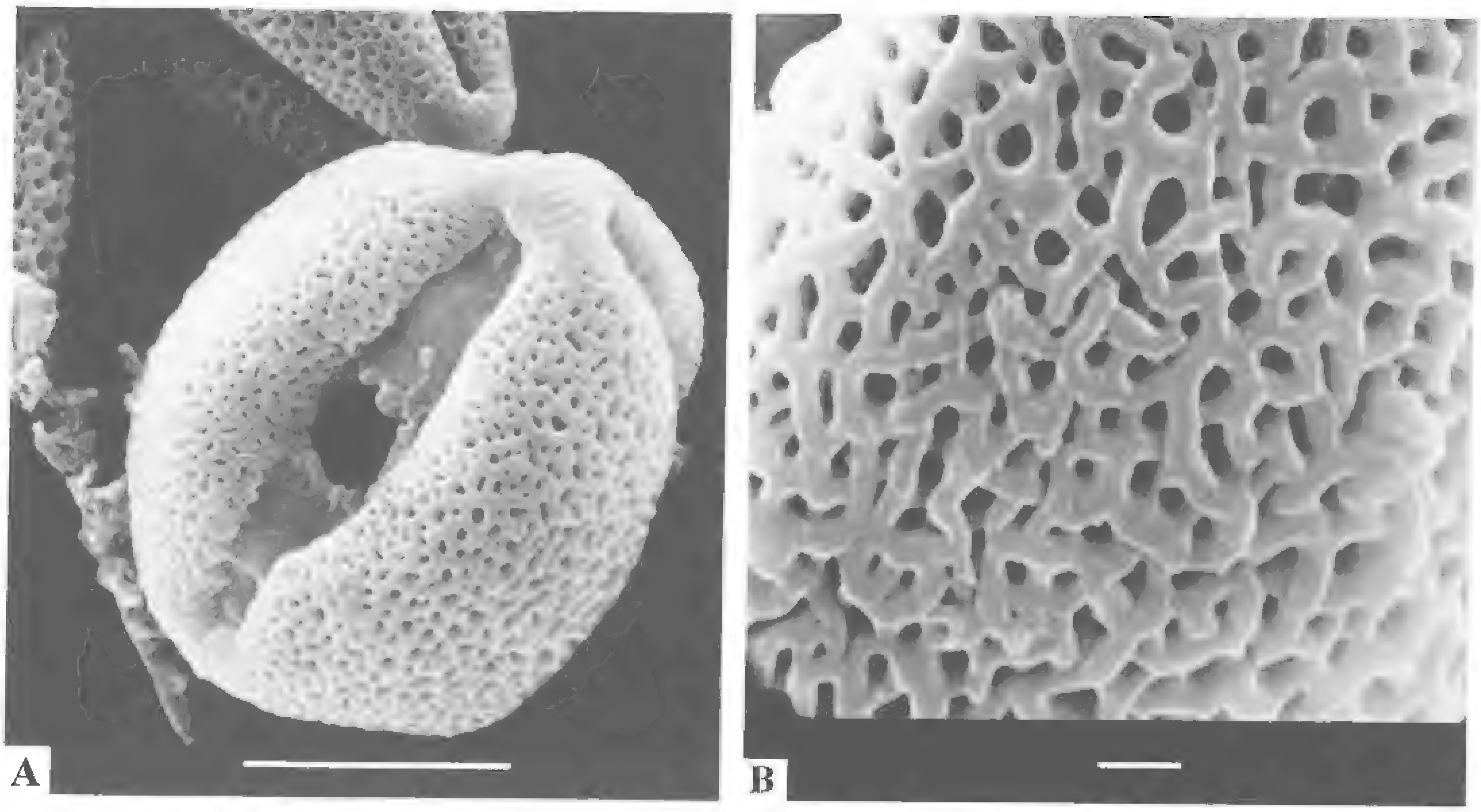


FIG. 4. Microfotografías SEM de polen de *Anisocapparis speciosa* (Griseb.) X. Cornejo & H.H. Iltis: A. escala 10 µm (*Vogel 483*, WIS). B. escala 1 µm (*R. de Michel 156*, WIS).

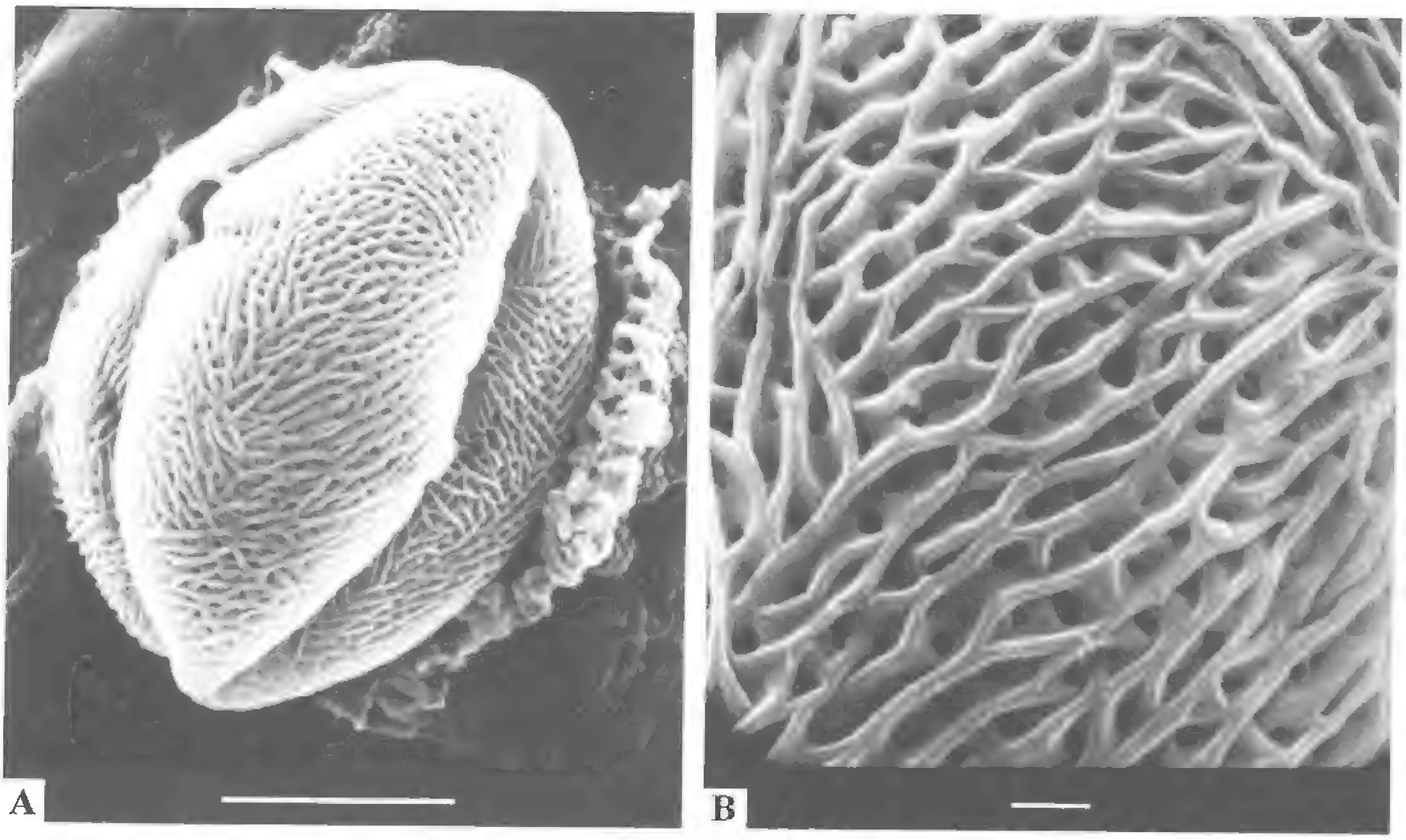


FIG. 5. Microfotografías SEM de polen de *Monilicarpa tenuisiliqua* (Jacq.) X. Cornejo & H.H. Iltis: A. escala 10 µm. B. escala 1 µm (*Gentry et al. 10992*, WIS).

frutos lineares a moniliformes de ápices delgado-atenuado, esencialmente sin pulpa, con semillas elipsoides dispuestas en una hilera (vs. frutos usualmente pepos, oblongos, cilíndricos, ovados u esféricos, con ápices ± redondeados, pocas veces agudos, pulpa[1] abundante hasta escasa y semillas cocleadas, dispuestas en dos ó más hileras).

Por sus frutos capsulares lineares-torulosos *Monilicarpa* se parece a *Cynophalla*, pero a más de los caracteres genéricos previamente mencionados, *Monilicarpa* fácilmente se diferencia de este último género por poseer flores con cálices 1-seriados (vs. cálices 2-seriados, decusados-imbricados), y vegetativamente por la ausencia de las glándulas nectarias axilares extraflorales (vs. presentes en *Cynophalla*) y la diferente filotaxia.

Algunos géneros distantemente relacionados a *Monilicarpa* como *Atamisquea* Miers, *Capparicordis* Iltis & Cornejo y *Colicodendron* Martius, también presentan tazas nectarias o nectarios cupulares, pero éstos fácilmente se diferencian de *Monilicarpa*, principalmente por presentar indumento de escamas lepídotas o tricomas estrellados, diferente tipo de polen y distintos tipos de frutos capsulares o amfisarcos, globosos hasta oblongos. Frutos lineares-torulosos también están presentes en algunas especies de *Quadrella* (DC.) J. Presl, un género ampliamente distribuido en las Indias Occidentales y América Central hasta el Sur de Florida hacia el norte y norte de Colombia y Venezuela hacia el sur (Iltis & Cornejo 2008). Pero *Monilicarpa* fácilmente se diferencia de *Quadrella* por ser glabra o presentar tricomas simples (vs. tricomas peltados hasta variadamente estrellados o candelabros), por la presencia de flores con cálices de sépalos fusionados hacia la base (vs. flores dialisépalas), hipantio presente (vs. ausente), nectario cupular o disciforme en cuyos bordes o pared externa se fusionan los pétalos (vs. presencia de cuatro escamas nectarias y pétalos insertos en un receptáculo plano).

Etimología.—El nombre *Monilicarpa*, alude a los delgados frutos moniliformes a linear-torulosos que presentan las especies de este nuevo género.

Monilicarpa y *Capparidastrum* son inermes (Cornejo & Iltis 2005b) y no presentan tallos generalmente espinosos, como ha sido reportado (Inocencio et al. 2006: 122, 125, ver *Capparis* sect. *Capparidastrum* y *Capparis brasiliana*).

CLAVE DE LAS ESPECIES DE *MONILICARPA*

1. Plantas deciduas o semideciduas, hojas pecioladas, espiraladas a lo largo del tallo; nectario floral cupular fusionado con el hipantio; semillas con embrión verde ____ **Monilicarpa tenuisiliqua**
1. Plantas sempervirentes, hojas subsésiles, subopuestas y/o 3-subverticiladas; nectario floral disciforme de bordes libres; semillas con embrión crema ____ **Monilicarpa brasiliana**

2.1. Monilicarpa tenuisiliqua (Jacq.) X. Cornejo & H.H. Iltis, comb. nov. (**Figs. 3A–C, 5**). Basónimo: *Capparis tenuisiliqua* Jacq., Enum. Pl. Carib. 24. 1760. *Pleuteron tenuis* Rafinesque, Sylva Tellur. 109. 1838. *Uterveria tenuisiliqua* (Jacq.) Bertol., Pl. Nov. Hort. Bonon. 2:8. 1839. *Capparidastrum tenuisiliquum* (Jacq.) Hutch., Genera Flowering Pl 2:310. 1967. Tipo: COLOMBIA: "Carthagenae frequens" (lectótipo, aquí designado: *Jacquin tab. 105* [en Select. Stirp. Amer. 2, 1763]).

Capparis obovatifolia Kunth, Nov. Gen Sp. 5:92. 1821. Tipo: VENEZUELA: Sucre, "crescit prope Cumaná. Fructificat Septembri," *A. Humboldt & A. Bonpland 93* (lectótipo, aquí designado: P!).

Capparis viridiflora Kunth, Nov. Gen. Sp. 5:92. 1821. Tipo: VENEZUELA: Sucre, "crescit prope Cumaná, in umbrosis. Floret Septembri," *A. Humboldt & A. Bonpland 569* (lectótipo, aquí designado: P!).

Colicodendron obovatum Turcz., Bull. Soc. Nat. Mosc. 27:327. 1854. Tipo: VENEZUELA: Carabobo, Puerto Cabello, Jun 1841 (fl), *H. Funck & L. Schlim 522* (lectótipo, aquí designado: G!; isótipos: BM!, LD!, P!).

Capparis garciae Dugand, Caldasia 1:45. 1941. Tipo: COLOMBIA: Cundinamarca, Mun. Tocaima, Hcda. Chucundá, matorrales, 16 Jul 1934 (fr), *H. García-Barriga 3109* (holótipo: COL-28357, foto de COL en WIS!, isótipo: NY!).

[1]En los especímenes de herbario algunas especies de *Capparidastrum* (e.g., *C. solum* [Macbr.] X. Cornejo & H.H. Iltis) parecen carecer de pulpa. Según observaciones en campo, estas especies en vivo poseen una escasa pulpa (de naturaleza arilar o en la cual la sarcotesta está infiltrada), que se reduce significativamente y/o desintegra durante el secado en el proceso de herborización.

Los lectótipos de *Capparis tenuisiliqua*, *C. obovatifolia*, *C. viridiflora* y *Colicodendron obovatum* son aquí designados debido a que ninguna colección fue referida bajo estas especies en las respectivas publicaciones originales. En el herbario US, *H. García-Barriga 3109* (1593366!) no constituye un isótipo de *Capparis Garciae*, ésta procede de una localidad distinta, Purificación, y fue colectada en diferente fecha, 7 Jul 1934.

Monilicarpa tenuisiliqua es una especie de hojas deciduas, su follaje se regenera durante la época de floración (*Smith 2100*).

Nombres locales.—COLOMBIA. Maretiro, Nudo, Palo de Agua (Dugand 1941: 44). VENEZUELA. Guariaro (*Aristeguieta 7014*), taparito (*Galué 167*).

Usos.—Para curar enfermedades, también para hacer cruces en Semana Santa (*L. Aristeguieta 7014*).

Especímenes representativos. **TRINIDAD & TOBAGO:** Patos Island, coastal bank, 13 Mar 1920 (fl), *N. Britton, T. Hazen & W. Medelson 533* (NY); ibidem, 5 Sep 1931 (fl), *R. Williams 12509* (NY). Chacachare, hillside, 3 Apr 1921 (fl), *N. Briton, W. Freeman & Sir F. Watts 2683* (NY). **COLOMBIA. Bolívar:** Vic. Cartagena, 1920 (fl), *Bro. Heriberto 362* (NY). **Magdalena:** Santa Marta, 3 mi. N of Bonda, 250 ft., 28 Apr 1898–1899 (fl), *H.H. Smith 2100* (NY[2]), 12 Jul 1898–1899 (fr), *H.H. Smith 843* (NY); S of Santa Marta, arid coastal belt, 5 Apr 1927 (fl), *E. Killip & A. Smith 21082* (NY). Don Jaca, 20 Jan 1930 (st), *S. Record 69, 80* (MAD, NY). Parq. Nac. Nat. Tayrona, Ensenada de Neguanje, 9 Sep 1976 (fr), *G. Lozano & R. Schnetter 2777* (NY), 21 Sep 1976 (fr), *G. Lozano & R. Schnetter 2926* (NY); dry slopes overlooking Caribbean, 11°20'S 74°02'W, 50 m, 23 Ago 1986 (fr), *A. Gentry & H. Cuadros 55485* (NY). Supra Honda, Río Seco, Dic 1852 (fr), *I. Holton s.n.* (NY). **VENEZUELA. Anzoátegui:** Fundo Lagunita de Flores, ca. caserío Curatiquiche, Barcelona, Mar 1969 (fl), *L. Aristeguieta 7014* (NY); Alrededores de Píritu, 18 Ago 1965 (fr), *G. Agostini 530* (NY). **Atlántico:** Entre Leña y Candelaria, 11 Ene 1941 (st), *A. Dugand & R. Jaramillo 2787* (COL, NY). Barranquilla, May 1927 (fl), *Bro. Elias 167* (NY). **Carabobo:** near Morón, rd. from Puerto Cabello to San Felipe, near sea level, 25 Apr 1920 (fl), *H. Pittier 8809* (NY). Around El Palito, near Puerto Cabello, 0–30 m, 2 Jul 1913 (fl), *H. Pittier 6427* (NY); ibidem, 1921(fr), *H. Pittier 9077* (NY); Puerto Cabello, 28 Sep 1874 (fl), *O. Kuntze 1747* (NY[2]); ibidem, 24 Jun 1917 (fl, fr), *H. Curran & M. Haman 1168* (NY); Distr. Colina, carr. Matarura-Guaibacoa, 19 Ago 1983 (fr), *T. Ruiz & T. Ruiz 4124* (MY, NY); Distr. Federal. Tacagua, May 1953 (fl). *L. Aristeguieta 1714* (NY). Fila de Machado, al O de Cabo Blanco, 10–100 m, 5 Ene 1964 (st.), *G. Agostini, M. Farinas & E. Castellanos 123* (NY); around Caracas, near El Portachuelo, 800–1000 m, 4 May 1922 (fl), *H. Pittier 10308* (NY). Puerto La Cruz, May 1961 (fl), *L. Aristeguieta 4642* (NY). Mun. Vargas, parroquia Catia La Mar, Escuela naval, 10°36'N 67°02'W, 5 m, 22 Mar 1988 (fl), *N. Ramírez 2493* (NY). **Falcón:** Dist. Silva, en escarpas calcáreas que miran al N a lo largo de Golfete de Guare, S de Chichiriviche, 10°54'N 68°16'–17' W, 1–10 m, 30 Ago 1974 (fl), *J. Steyermark & B. Manara 110864* (NY); Distr. Colina, carr. Mataruca Guaibacoa, 120 m, 20 Dic1981 (fl, fr), *T. Ruíz & F. Rondón 3641* (MY, NY); Distr. Federación, Caserío los Botalones, vía Churuguara, 680 m, *T. Ruiz & F. Rondón 3823* (MY, NY). **Guárico:** Altagracia de Orituco-Chaguaramas, Mar 1966 (fl), *L. Aristeguieta 6057* (NY[2]). **Lara:** Barquisimeto, Terepaima, 25 Abr 1968 (fl), *G. Ferrari, L. Cárdenas & G. Bunting 313* (MY, NY); near Centro Comercial los Leones, 30 Apr 1974 (fl), 540 m, *A. Gentry, G. Morillo & B. de Morillo 10992* (NY, WIS); Distr. Palavecino, laderas pendientes entre Terepaima y Cabudare, 500–900 m, 5, 10 Ago 1970 (fr), *J. Steyermark, F. Delascio, G. K. & E. Dunsterville* 103633-A (NY). **Mérida:** Chama Valley, near Estanques, 470 m, 9 Ene 1965 (fr), *F. Breteler 4559* (NY). **Nueva Esparta:** Island of Margarita, El Valle, 13 Jul 1901 (fl), *O. Miller & J. Johnston 9* (NY); ibidem, 150 m, 21 Jul/8 Ago 1903 (fl, fr), *J. Johnston 6* (NY). **Sucre:** Cerca de Cumaná, entre Puerto La Cruz y Cumaná, Jul 1964 (fr), *L. Aristeguieta 5372* (NY). **Tachira:** S of la Mulata, near Venezuelan-Colombian border, 72°27'30"W 7°50'30"N, 300 m, 13 Nov 1979 (fr), *J. Steyermark, R. Liesner & A. González 120231* (NY). **Zulia:** Distr. Urdaneta, hcda. El Zanjón, km 10 entre Porterito y Los Claros, 5 Oct 1982 (st), *N. Galué 167* (NY); Distr. Miranda, vía que conduce entre las carr. Lara-Zulia y Coro-Maracaibo, que desvía sobre la Lara-Zulia en km 8 SE del Puente sobre el lago, 4 Mar 1979 (fl), *G. Bunting 7183* (NY); Distr. Betijoque, carr. Agua Viva-Valera, en km 4 al S de Motatán, lado derecho de la vía, ca. 400 m, 31 May 1981 (fr), *G. Bunting 9938* (NY).

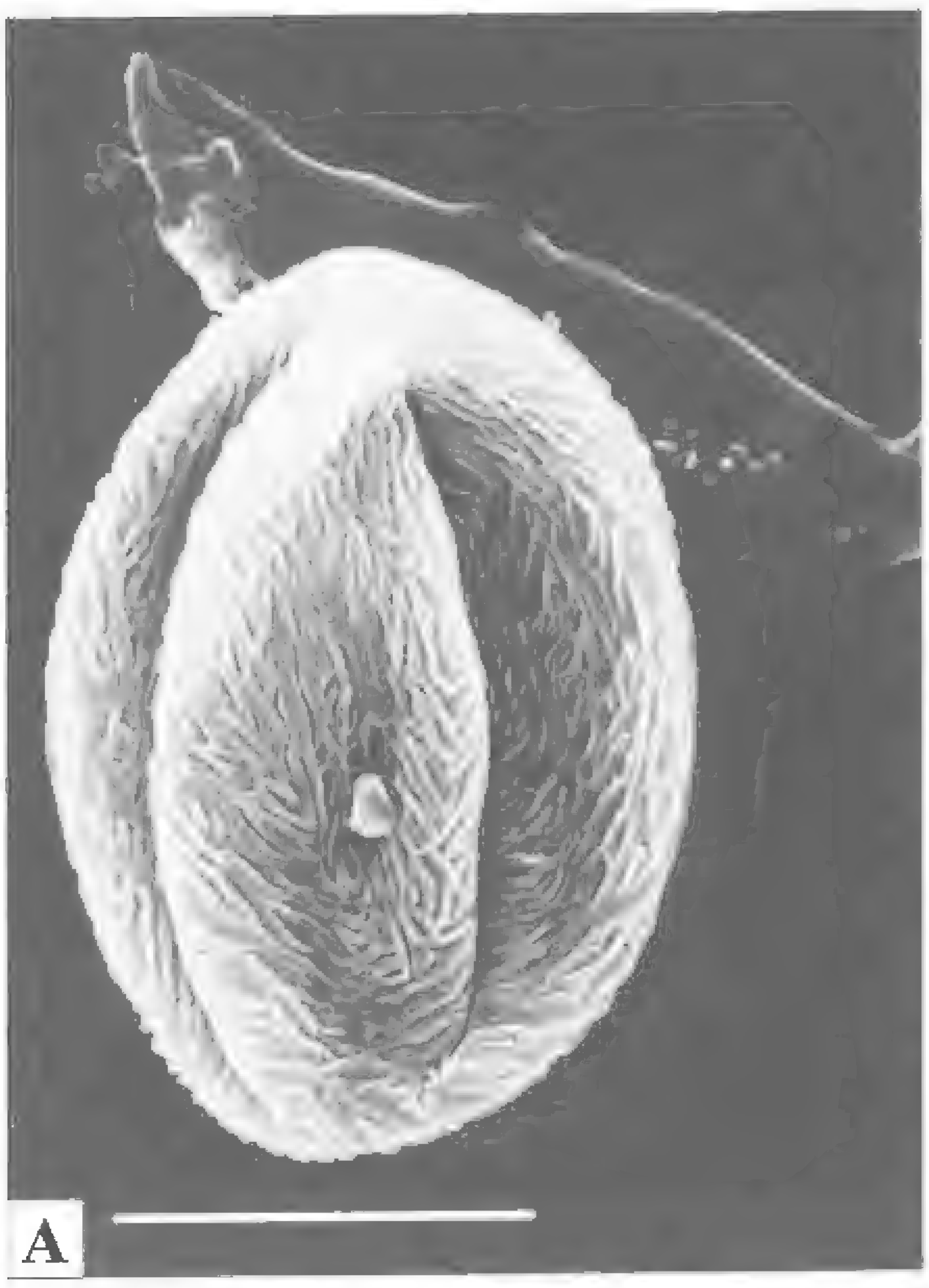
2.2. Monilicarpa brasiliana (Banks ex DC.), X. Cornejo & H.H. Iltis, comb. nov. (**Figs. 3D–E, 6**). Basónimo: *Capparis brasiliana* Banks ex DC., Prodr. 1:249. 1824. *Capparidastrum brasilianum* (Banks ex DC.) Hutch., Gen. Fl. Pl. 2:310. 1967. Tipo: BRASIL: Brasilia prope Rio de Janeiro, 1768, *J. Banks & D. Solander s.n.* (lectótipo, aquí designado: BM!; isótipo: MO-1611720!).

Capparis brasiliana var. *longipes* A. Gray, in Wilkes, C., U.S. Explor. Exped. 15:68. 1854. Tipo: BRASIL: Guanabara, Rio de Janeiro, 1838–1842, *C. Wilkes et al. s.n.* (lectótipo, aquí designado: US- 63413!).

Capparis verticilaris Turcz, Bull. Soc. Nat. Mosc. 36:552. 1863. Tipo: BRASIL: Brasilia, *Sellow 700* (B?).

Nombres locales.—BRASIL. Feijão-de-boi (Fuks & Costa e Silva 2000: 6).

Especímenes representativos. **BRASIL. Bahia:** Ipuaçu Cachoeira/Bahia-Vale dos Rios, Paraguacu/Jacuipe, ca. 39°05'W 12°32'S, 40–120 m, Sep 1980 (fl), *Pedro do Cavalo et al. 738* (NY); Itambé, Rod. BA-415 Itapetinga/Itambé, 20,4 km 15°16'1" 40°25'17"W, 3 Nov 2000 (fl), *J. Jardim, S. de Santana & F. Juchum 3159* (NY). **Espirito Santo:** Cachoeiro da Itapemirim, Morro Grande, a 3 km W da saida da cidade na rodovia para Jerônimo Monteiro (BR-482), 9 Dic 1994 (fl), *J. Pirani, M. Magenta & A. Conceição 3519* (NY, WIS). **Rio de Janeiro:** Rio de Janeiro, Guanabara, Recreio dos Bandeirantes, Ago 1961 (fr), *A. Duarte 6244* (MO, NY); Morro da Gamboa, Cabo Frio, 7 Oct 1968 (fl), *D. Sucre 3794* (NY); Entre Barra de S. Joao e Tamoios, 28 Sep 1964 (fl), *E. Santos, B. Flaster (1103) & C. Pereira 2066* (WIS [3]).



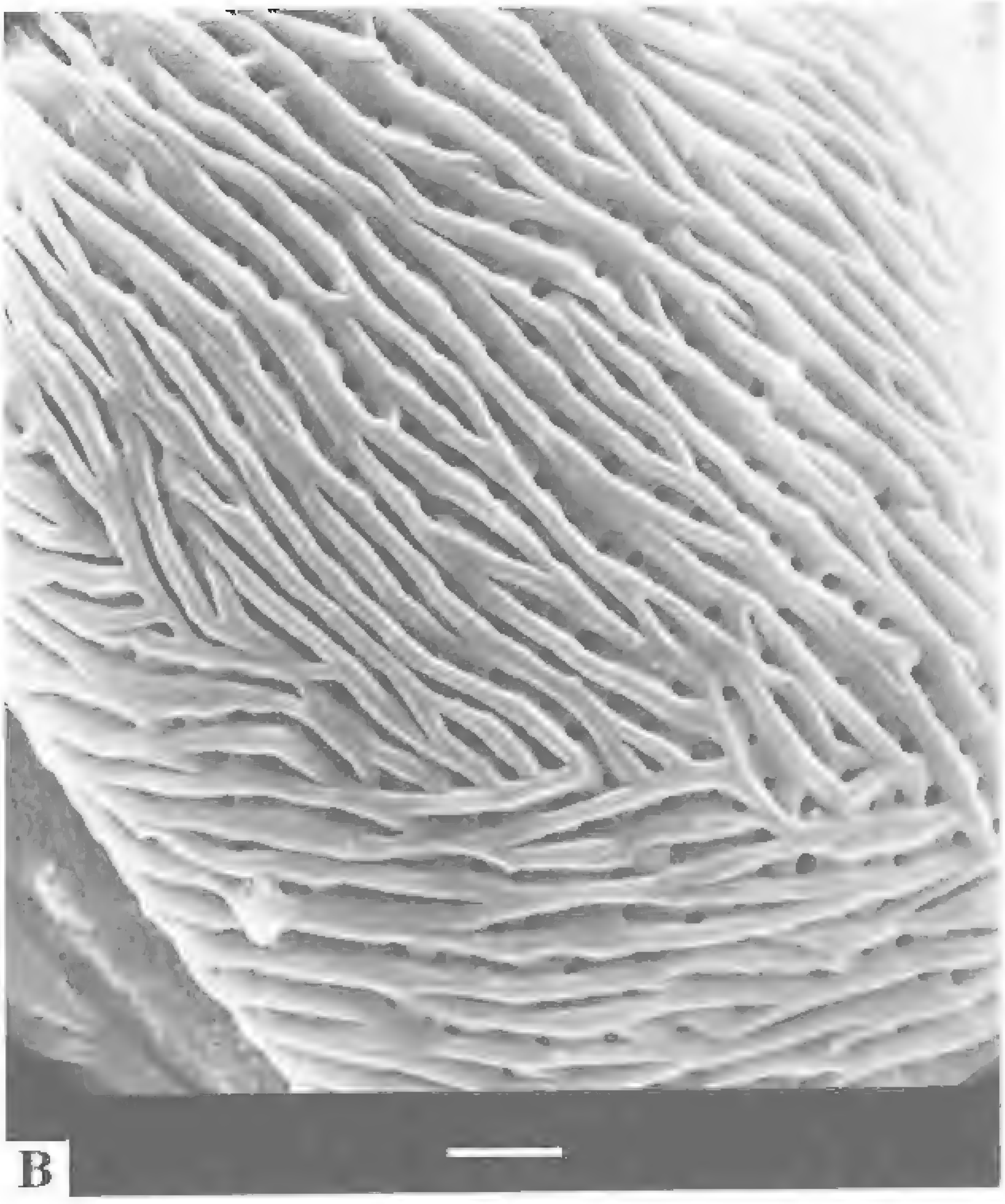
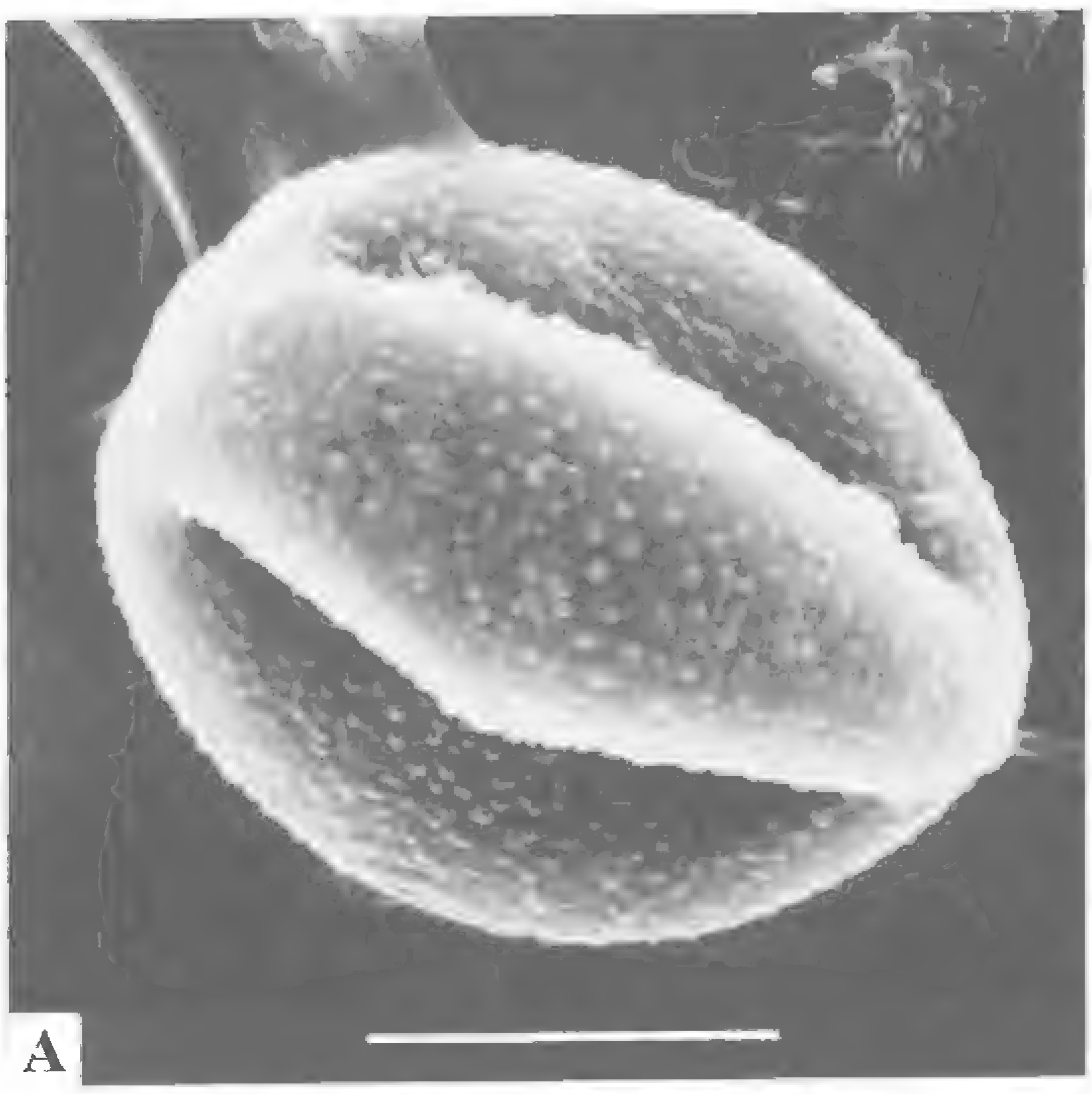


Fig. 6. Microfotografías SEM de polen de *Monilicarpa brasiliana* (Banks ex DC.) X. Cornejo & H.H. Iltis: **A.** escala 10 µm. **B.** escala 1 µm (*Santos et al. 2066*, WIS).



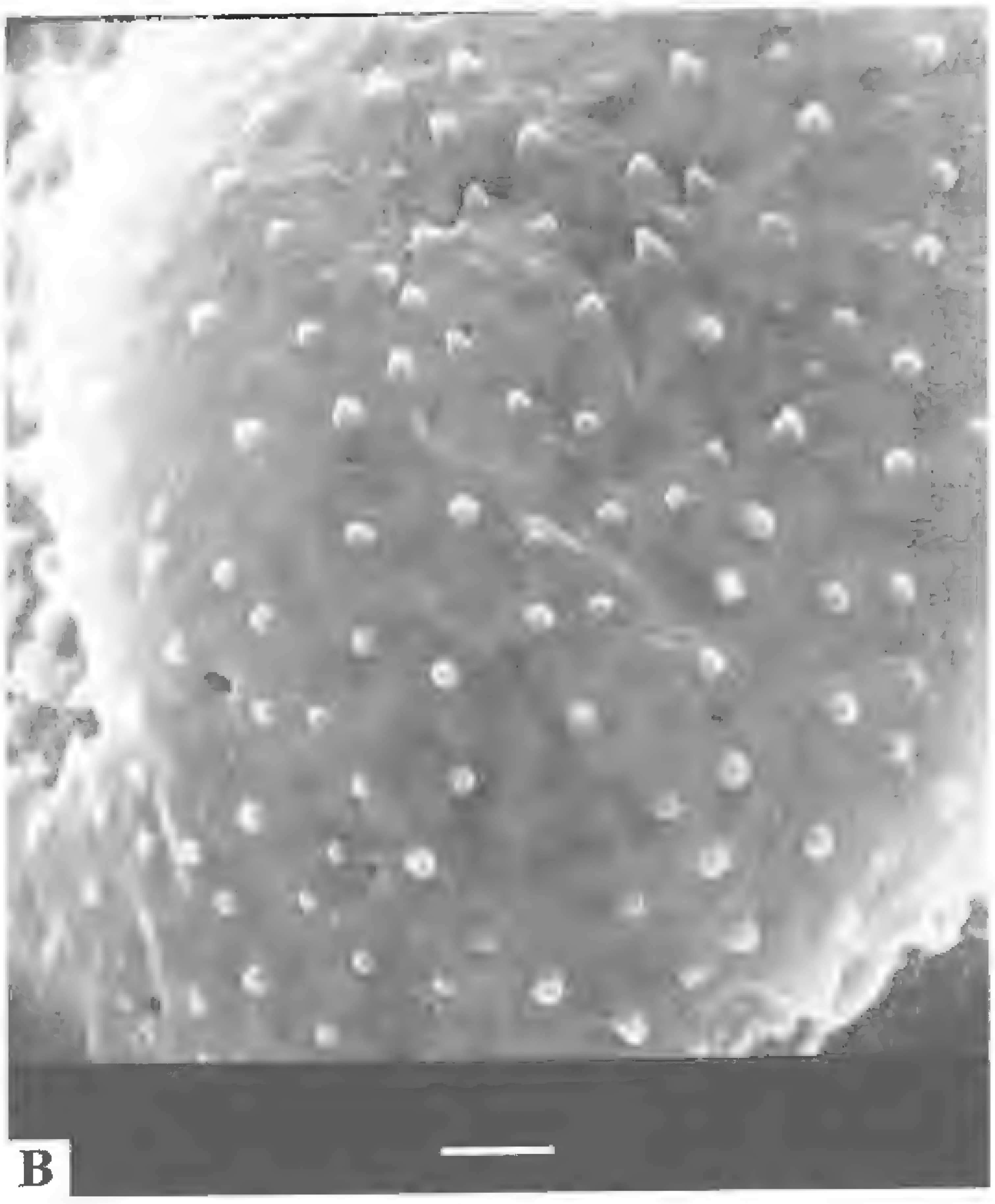


Fig. 7. Microfotografías SEM de polen de *Capparidastrum* Hutch.: **A.** escala 10 µm. **B.** escala 1 µm (*Mori & Kallunki 5379*, WIS).

CLAVE DE LOS GÉNEROS DE CAPPARACEAE DE HOJAS SIMPLES, GLABROS O CON PUBESCENCIA SIMPLE EN AMÉRICA

1. Nectarios extraflorales presentes, dispuestos supraxilarmente en las ramas terminales y en las ramas laterales; nectarios florales planos hasta un poco cóncavos, dispuestos horizontalmente sobre el receptáculo, escamas nectarias pocas veces rudimentarias o más bien ausentes; hojas dísticas (excepto *Cynophalla sclerophylla*), con peciolos de similar longitud, pulvínulo ausente; frutos capsulares (dehiscentes); semillas con embrión clorofílico, verde ______ **Cynophalla** (DC.) J. Presl
1. Nectarios extraflorales ausentes; nectarios florales carnosos dispuestos sobre el receptáculo y usualmente redondeados o escamas nectarias erectas o nectarios florales cupulares o disciformes; hojas subopuestas y/o 3-subverticiladas o usualmente espiraladas, las grandes frecuentemente con peciolos pulvinados y de diferentes longitudes a lo largo de las ramas (a menudo no obvio en los especímenes de herbario); frutos pepos, anfisarcos (indehiscentes) o capsulares (dehiscentes); semillas usualmente con embrión no clorofílico, usualmente blanco o crema, rara vez amarillo o verde (en *Monilicarpa tenusiliqua*).
   2. Cáliz con sépalos de similar longitud, frecuentemente 1-seriado; nectarios florales isomórficos constituidos por cuatro glándulas carnosas, usualmente redondeadas o cuatro escamas nectaríferas o una nectario cupular o disciforme dentro de un pequeño hipantio; granos de polen con ornamentación tectada-espinulosa, tectada-perforada o estriada-reticulada; semillas cocleadas hasta elipsoides, embriones convolutos, delgados y flexibles (en vivo), cotiledones de tamaños similares hasta algo asimétricos.
      3. Brácteas de- y/o cerca de- la base del pedúnculo de las inflorescencias, si presentes, frecuentemente triangulares, usualmente < 2 mm; nectarios florales constituidos por cuatro glándulas carnosas, usualmente redondeadas, usualmente insertas sobre un receptáculo plano y/o a veces fusionadas hacia la base del androginóforo; pétalos insertos en un receptáculo ± plano; filamentos de los estambres insertos en varios verticilos alternos sobre una superficie convexa hasta hemisférica en la parte superior del andróforo (observable en la antesis, en material fresco o en vivo); granos de polen con ornamentación tectada-espinulosa o tectada-perforada; frutos usualmente oblongos hasta elípticos o globosos, con ápices ± redondeados, pocas veces agudos, con pulpa ± presente (a veces escasa en vivo, que se reduce o desintegra al secar) y con semillas cocleadas o reniformes dispuestas en dos ó más hileras, cotiledones simétricos ______ **Capparidastrum** Hutch.
      3. Brácteas de- y/o cerca de- la base del pedúnculo de las inflorescencias frecuentemente presentes, lineares, hasta 13 mm; nectarios florales cupulares o disciformes dentro de un pequeño hipantio; pétalos fusionados en el borde o en la parte externa de un nectario floral cupular o disciforme; filamentos de los estambres insertos en dos verticilos alternos en un adroginóforo apenas engrosado; granos de polen con ornamentación estriada-reticulada; frutos moniliformes o lineares-torulosos, con ápices delgado-atenuados, esencialmente sin pulpa y con semillas elipsoides dispuestas en una hilera y separadas por las constricciones de las paredes del futo, cotiledones algo asimétricos (jacknife) ______ **Monilicarpa** X. Cornejo & H.H. Iltis
   2. Cáliz anisosépalo, distintivamente 2-seriado y decusado-imbricado desde las prefloraciones jóvenes, con dos sépalos externos de menos de la mitad del tamaño que los dos sépalos internos; nectarios florales constituidos por cuatro escamas episépalas fuertemente dimórficas (dos menores y dos mayores); granos de polen con ornamentación finamente reticulada; semillas subglobosas, embriones fuertemente anisocótilos, con un cotiledón mayor subgloboso y compacto, especializado para almacenar y uno menor muy reducido o ausente ______ **Anisocapparis** X. Cornejo & H.H. Iltis

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A REVISION OF *COLICODENDRON* (CAPPARACEAE)

Xavier Cornejo
The New York Botanical Garden
200th St. and Kazimiroff Ave.
Bronx, New York 10458-5126, U.S.A.
xcornejo@nybg.org, xcornejoguay@gmail.com

Hugh H. Iltis
Department of Botany
University of Wisconsin, 430 Lincoln Drive
Madison, Wisconsin 53706, U.S.A.
swis@charter.net

ABSTRACT

The South American genus *Colicodendron* (Capparaceae) is validated and amended. The taxonomic limits and the generic relationships are established and discussed. *Colicodendron* consists of four species, the previously established *Colicodendron yco* Mart. from northeastern Brazil, and *C. scabridum* (Kunth) Seem. from western Ecuador and Perú, plus two new species herewith described: 1) **Colicodendron bahianum** X. Cornejo & H.H. Iltis, restricted to the Atlantic coastal rainforests of the State of Bahia, eastern Brazil; and, 2) **Colicodendron valerabellum** H.H. Iltis, T. Ruiz & G.S. Bunting, a local endemic from the dry shrublands and forests in the environs of Valera, in the State of Trujillo, Venezuela. The new species are illustrated, a map and a key to the species of *Colicodendron* are herewith provided.

RESUMEN

Se valida y enmienda *Colicodendron* Mart., un género de Capparaceae restringido a América del Sur. Se establecen sus límites taxonómicos y se discuten sus relaciones con géneros afines. *Colicodendron* está representado por cuatro especies: Las previamente establecidas *Colicodendron yco* Mart., distribuida al noreste de Brasil, y *C. scabridum* (Kunth) Seem., localizada en los bosques secos y xerofíticos al oeste de Ecuador y norte de Perú; más dos nuevas especies aquí descritas: 1) **Colicodendron bahianum** X. Cornejo & H.H. Iltis, sólo conocida de los bosques húmedos del Estado de Bahía, al este de Brasil. Y, 2) **Colicodendron valerabellum** H.H. Iltis, T. Ruiz & G.S. Bunting, una endémica local restringida a los bosques secos del área de Valera, en el Estado Trujillo, Venezuela. Se ilustran las nuevas especies y se provee de una clave y mapa para las especies de *Colicodendron*.

Key Words: *Colicodendron*, Capparaceae, Brazil, Ecuador, Perú, Venezuela, endemics

During our studies of the neotropical species of *Capparis* s.l. (Capparaceae), carried out to produce a generic realignment of this extremely polymorphic genus, it became clear that *Colicodendron* Mart. is a well defined South American genus of stellate shrubs and trees, characterized by having a 1-seriate valvate calyx with a dentate or lobed nectary-dish or nectary-cup, and thick-walled, indehiscent amphisarcous fruits.

Colicodendron was established by Martius (1839: 25), for two Brazilian species: *Colicodendron yco* Mart., the generic type, and *C. longifolium* Mart. (the latter recently placed in *Neocalyptrocalyx*, as *N. longifolium* [Mart.] X. Cornejo & H.H. Iltis [2008a]). Subsequently, Seeman (1852: 78) correctly transferred to *Colicodendron*: *Capparis scabrida* Kunth, but also the unrelated *Capparis avicennifolia* Kunth, and *Capparis pulcherrima* Jacq. (the latter as *Colicodendron pulchellum* Seem., nom. reject.), as well as the quite unrelated glabrous or simple-haired *Capparis subbiloba* Kunth (=*Cynophalla flexuosa* [L.] J. Presl). Two years later, Turczaninow (1854: 327–328) erratically described three species in *Colicodendron*, all of them synonyms of unrelated species of *Capparis* s.l., a contribution that obfuscated any clear concept of that genus.

Colicodendron was treated as a subgenus of *Capparis* L. s.l. (Eichler 1865: 272), and later as a section of *Capparis* (Pax & Hoffmann 1936: 181). In both mentioned infrageneric taxa, the members of *Colicodendron* were mixed up in a heterogeneous assemblage with the Mexican *Capparis angustifolia* Kunth (= *Quadrella angustifolia* [Kunth] H.H. Iltis & X. Cornejo), and the South American *C. crotonoides* Kunth and *C. tweediana* Eichler (both members of *Capparicordis* H.H. Iltis & X. Cornejo, a recently described stellate neotropical genus, Iltis & Cornejo 2007). Most recently Hutchinson (1967: 309), in his attempted generic realignment of *Capparis* s.l., made seven additional, but all inappropriate combinations to produce a poorly defined *Colicodendron*.

In this work, a revision of *Colicodendron* is presented. The genus is validated and amended, its morphological limits are defined, and the relationships with the morphologically closely related genera are discussed.

Colicodendron Mart., Flora 22, Bleibl. 1:25. 1839, emend. X. Cornejo & H.H. Iltis. Type: *Colicodendron yco* Mart.

Destrugesia Gaudich., Bot. Voy. Bonite, t. 57. 1844–1846. Type: *Destrugesia scabrida* Gaudich.

Evergreen shrubs or trees, covered by stellate to echinate trichomes throughout. Leaves simple, short-petiolate to sessile, opposite to spirally or whorled. Inflorescences terminal, subterminal and/or axilar, a panicle, raceme or racemose spike, rarely a solitary axillary flower (in *Colicodendron yco*); floral bracts filiform or subulate, deciduous. Flowers with calyx 1-seriate, valvate, ± cup-shaped, the 4 sepals free, ± equal, distinct and entirely enclosing the corolla in bud, their margins and tips touching each other from early bud until near anthesis, at the base fused forming a hypantium, coated by a 4-dentate nectary dish or nectary cup or a 3-lobed nectary cup within. Petals 4, imbricate or torsivus in bud, sessile. Stamens 14 to 60, the filaments geniculate or spirally arranged in bud, at anthesis exserted, inserted on an expanded flat androgynophore, anthers basifixed. Fruits amphisarcous or pseudoamphisarcous (in *C. scabridum*), woody, thick-walled and multilocular, bearing white- or yellow-embryoned seeds, ca. 1–2 cm, cotyledons ca. 1–1.5 mm wide, convolute, testa crustaceous.

Due to the stellate pubescence, 1-seriate valvate calyx with the lobes covering the corolla from early bud until near anthesis, and the presence of a nectary cup or nectary dish, *Colicodendron* is related to the recently described neotropical genus *Capparicordis* H.H. Iltis & X. Cornejo. However, *Colicodendron* differs from the latter by having elliptic, lanceolate, oblong to oblanceolate, pinnately nerved leaf blades (vs. cordate to reniform or suborbicular and basally subpalmatly-nerved leaf blades); a 4-dentate nectary dish or 3-lobed nectary cup (vs. a nectary cup with four filiform to triangular-filiform appendages); higher number of stamens, 14 to 60 (vs. 4 to 8); and larger indehiscent thick-walled amphisarcous fruits, with an inflexible woody pericarp bearing larger seeds, ca. 1–2 cm (vs. smaller dehiscent fruits, with a soft and flexible, thinly coriaceous pericarp, which splits and falls off at maturity, bearing smaller seeds, ca. 5–7 mm, dispersed by birds, Cornejo pers. obs., 2002). *Colicodendron* is also related to the South American genus *Calanthea* (DC.) Miers, as was correctly stated by Martius in the original publication (p. 27, cf. with *Capparis pulcherrima* Jacq., the type of *Calanthea* [DC.] Miers). However, *Calanthea* mainly differs from *Colicodendron* by the very distinctive calyx with open aestivation, in which the not valvate linear-ligulate sepals are widely spaced from each other, exposing a valvate corolla from the very young bud; and by the seeds with barely folded, very thick cotyledons, 4–7 mm wide (Cornejo & Iltis 2008b).

Colicodendron could be also related to the stellate to peltate, Central American-West Indian genus *Quadrella* (DC) J. Presl. However, *Colicodendron* differs from the latter by having flowers with a hypanthium coated by a nectary dish or nectary cup (vs. flowers without hypanthium, but with a flat receptacle and four scales inserted on it in *Quadrella*); and indehiscent, ellipsoid to globose thick-walled woody amphisarcous fruits with larger seeds (vs. capsular, dehiscent, linear or oblong and few times to ovoid, with seeds distinctively smaller, usually arranged in a single row in *Quadrella*).

Colicodendron was previously known by two widely disjunct endemic species: *Colicodendron yco* from eastern Brazil, and *C. scabridum* (Kunth) Seem., restricted to the dry forests of western Ecuador and adjacent Peru. In this work, two additional South American endemic species, both with whorled subsessile leaves and beautiful inflorescences are added to this genus.

1. Colicodendron bahianum X. Cornejo & H.H. Iltis, sp. nov. (**Figs. 1, 2, 7**). Type: BRAZIL. Bahia: Antiga rodovia que liga a Estacion Ecologia do Pau – Brasil a Sta. Cruz, 7 km ao NE da estacao, ca. 12 km ao NW de Porto Seguro, 16°23'S 39°8'W, Regiao de Mata Higrofila Sul Baiano, ca. 80–100 m, 14 Aug 1979 (fl), *S.A. Mori, L.A. Mattos Silva & S.A. Euponino 12710* (holotype: CEPEC; isotypes: NY, US, WIS).

Colicodendrum species novum cum pubescentia stellata, calyx valvatis 1-seriatis cum nectarius cupularibus et fructus amphysarcum, affinis *Colicodendrum yco* Mart., a qua differt frutex pauciramosis cum foliis subverticillatis et subsessilis (nec ramosissimis cum foliis oppositis et petiolatis), inflorescentiis racemosiis (nec paniculatiis), staminis 30 ad 42 (nec 14 ad 20), gynophoriis 1.6–2 cm longiis, glabriis (nec gynophoriis 3.5–5 cm longiis et stellatiis pubescentiis).

Sparsely branching shrubs or slender treelets, 1–6 m × 4 cm dbh; terminal branches densely stellate-echinate; stipules absent. Leaves subverticillate, grouped in whorls at the end of the terminal branches, sessile or

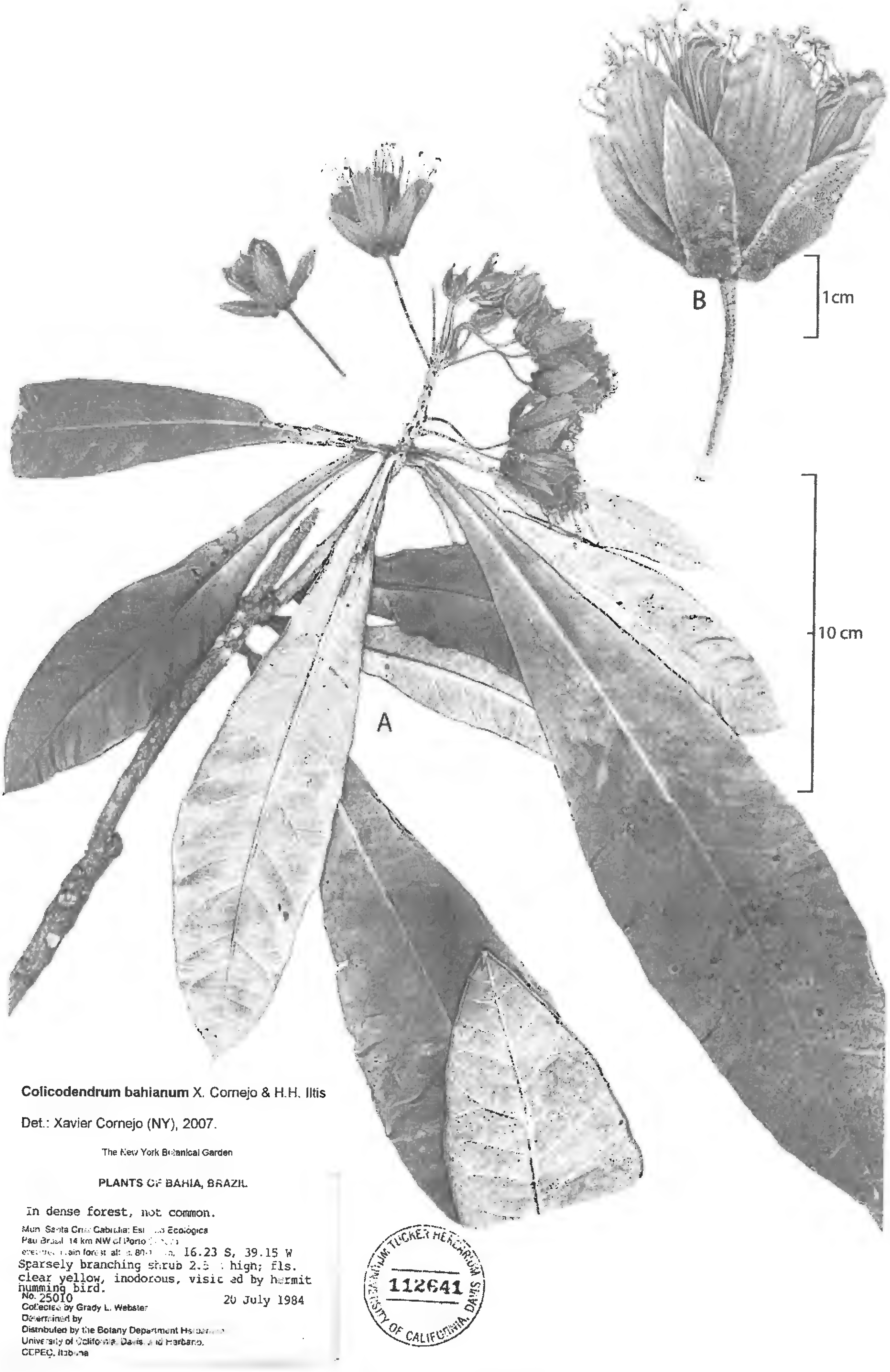

FIG. 1. *Colicodendron bahianum* X. Cornejo & H.H. Iltis. A. Terminal branch with whorled leaves and terminal inflorescence. B. A flower nearly to anthesis. (A, B. *G. Webster 25010*, DAV).

subsessile, with blades narrowly oblanceolate to narrowly elliptic, 13–40 × 3–7(–10) cm, stiff, coriaceous (alive), chartaceous (dry), attenuate and revolute at the base, acute and apiculate to sometimes shortly rostrate at the apex, shiny green (alive) with an impressed to often sulcate midvein, nerved and glabrous above, paler green (alive) and with a strongly prominent glabrous or echinate-stellate midvein beneath, margin inconspicuosly thickened, with 15 to 25 major upward-arching lateral nerves on each side of the midvein. Inflorescences terminal and subterminal racemes, sometimes cauliflorous in older wood, densely stellate-echinate; axis short, 1–5 cm, stout, bearing to 25 flowers at the same time. Floral bracts linear, 3–7 mm, deciduous, densely echinate-stellate. Pedicels 1.8–4 cm, articulate to the axis. Sepals oblong-elliptic or ellipsoid to lanceolate, 12–22 × 6–8 mm, abaxially keeled, mainly toward the base, ± acute at apex, yellow (alive), rusty brown (when dry), stellate-echinate abaxially; hypanthium 4–6 mm deep, coated by a subtetragonal 4-dentate nectary dish within, nectary appendages broadly deltoid to semiorbicular, 1.5 × 2.5–4 mm, glandular, stellate. Petals torsivae in bud, apparently inserted at the edge of the nectary cup, oblong to obovate-oblong, 20–28 × 7–12 mm, widely obtuse to rounded at apex, longitudinally nerved, sulfur yellow and erect at anthesis (Mori, pers. com.), dull rusty-brown (when dry), stellate on both sides. Stamens 30 to 42, filaments 2–3 cm, geniculate in bud, glabrous, inserted on a white-stellate-tomentose expanded torus-like androgynophore, anthers ca. 2 mm, white (alive). Gynophore 1.6–2 cm, glabrous; ovary oblong, 5–6 × 2–3 mm, longitudinally sulcate, glabrous; stigma sessile, capitate. Infructescences with gynophores ca. 2–2.5 × 0.3–0.5 cm, pedicels ca. 3–3.5 cm. Amphisarcous oblong-ellipsoid, 7–12 × 2–4 cm, subpendulous; fruit wall 3–7 mm thick, mature seeds 1.3–1.7 mm in diam.

Colicodendrum bahianum is somewhat related to the equally yellow-flowered *C. yco*, is allopatric in the dry Caatinga to the north (Fig. 7). However, the more mesophytic *C. bahianum* can be easily distinguished by dense whorls of subsessile leaves, arranged toward the end of the terminal branches (Fig. 1A, vs. subopposite and pedicellate leaves, more spaced out along the branches). The inflorescences of *Colicodendrum bahianum* are short dense racemes (vs. larger and longer, paniculate inflorescences, or rarely solitary axillary flowers in *C. yco*), bearing flowers with erect (vs. reflexed) sepals at anthesis, higher number of stamens (30 to 42 vs. 14 to 20 in *C. yco*), smaller anthers (ca. 2 mm vs. 4 mm), shorter glabrous gynophores (1.6–2 cm vs. 3.5–5 cm, pubescent) and glabrous (vs. pubescent) ovaries.

Due to the whorled subsessile leaves, *Colicodendron bahianum* seems morphologically more closely related to the herein also described *Colicodendron valerabellum* H.H. Iltis, T. Ruiz & G.S. Bunting (for differences see comment under the latter species).

Phenology.—Collected in flower in February, July, August, November and January, and fruit in August. The sulfur yellow flowers are visited by hermit hummingbirds (*Webster 25010*).

Cytology.—Unknown.

Distribution.—Eastern Brazil, restricted to the southern extension of the moist or wet evergreen Atlantic rain forests (ca. 2000 mm) into southeastern Bahia State (Fig. 7).

Conservation concern.—Habitat is under intense human pressure from both agriculture and wood harvesting, especially for so decorative species *Colicodendrum bahianum* (Scott Mori, per. comm., Sep 1979; "It was one of the most beautiful species that I've ever seen"). Images of this potential ornamental species are available at the New York Botanical Garden Web site (NYBG, 2003).

Paratypes. **BRAZIL. Bahia:** Mun. Santa Cruz Cabrália, mata costeira, 15 Jul 1966, *R.P. Belem & R.S. Pinheiro 2580* (F, UB, WIS). Est. Ecológica Pau Brazil, 14 km NW of Porto Seguro, evergreen rainforest, 39°15'W 16°23'S, ca. 80–100 m, 20 Jul 1984, *G.L. Webster 25010* (CEPEC, DAV, WIS). Porto Seguro, Parq. Naca. Monte Pascoal, 15 Jan 1973 (fl.), *T.S. Santos 2692* (CEPEC, NY, WIS); ibidem, trail to peak, upper slopes and top of Monte Pascoal, 40°34'29"W 15°15'53"S, 250–536 m, 14 Nov 1996, *W. Thomas et al. 11256* (NY). Estrada a Santa Cruz, Itaju do Colônia, 15 Jan 1971 (fl), *T.S. Santos 1329* (CEPEC, WIS). Guaratinga, plantacao de Cacau, 10 Aug 1966, *R.P. Belem & R.S. Pinheiro 2749* (UB, WIS). Potiraguá, Fazenda Independencia, Rod. Itaimbe, Potiraguá, ca. 15 km a partir da BR 101, 15°42'12"S 39°34'31"W, 6 Feb 2004, *P. Fiaschi et al. 2283* (CEPEC, NY [NY photo in WIS]). Pastaria, Itaimbe – Potiraguá, 10 Nov 1967, *R.S. Pinheiro 414 & T.S. Santos 77* (CEPEC, UB, WIS). Potiraguá a Itaimbe km. 10, 29 Jan 1972, *R.S. Pinheiro 1801 [1802]* (CEPEC, WIS); km 10 da rod. Potiraguá para Itaimbé; 24 Jul 1973, *R.S. Pinheiro 2202* (CEPEC, WIS). Entre Eunápolis et Tabela, ± km 15, 28 Nov 1970, *E. de Mello Filho 2988 & M. Emmerich 3526* (CEPEC [CEPEC photo and fragm. at WIS]). "Mun. Itabello, Bahia" [there is no such place, perhaps a mistake

for Itabuno, a prominent town in the Cacao region, where the CEPEC herbarium is located], Cascalheira, mata pluvial, 13 Aug 1995 (fl, fr), *C. Hatschbach, M. Hatschbach & J.T. Motta 63068* (US [US photo at WIS]).

2. Colicodendron scabridum (Kunth) Seem., Bot. Voy. Herald 78. 1852. (**Fig. 7**). Basionym: *Capparis scabrida* Kunth, Nov Gen. Sp. 5:95. 1821. *Octanema scabrida* Rafin., Sylva Tellur. 112. 1838. *Destrugesia scabrida* (Kunth) Gaudichaud, *nomen*, *Voyage de La Bonite* [text unpubl.], Atlas pl. 57. 1842. *Colicodendron scabridum* (Kunth) Hutch., Gen. Fl. Pl. 2:309. 1967, hom. illeg. Type: ECUADOR or PERU: *Habitat in America meridionali*, without data, *Humboldt & Bonpland s.n.* (lectotype, designated here: P [microfiche at NY!]; isolectotype: B-W 10055-01 0! [B-W photo 9478 at WIS!]).

Capparis angulata Ruiz & Pav. ex DC., Prodr. 1:253. 1824. *Colicodendron angulatum* (Ruiz & Pav.) Hutch., Gen. Fl. Pl. 2:309. 1967. *Capparis canina* Tafalla, *nomen*. Type: ECUADOR: Guayas, Guayaquil, 1799 (fl), "Zapote de perro," *Ruiz s.n.* (=*Tafalla*) (lectotype, designated here: MA [MA photo 29269 at WIS!]; isolectotypes: B 10 0242738! [B photo 342 at WIS!], G! [G fragm. at WIS!]).

Capparis gaudichaudiana Eichl. in Mart, Fl. Bras. 13:273. 1865. *Colicodendron gaudichaudianum* (Eichl.) Hutch., Gen. Fl. Pl. 2: 309. 1967. Type: PERU: Piura, Paita, *Voyage de la Bonite*, Jul 1836 (fl, fr), *M. Gaudichaud s.n.* (lectotype, designated here: B 10 0242739!; isolectotypes: B 10 0242737! ["misit 1841"]; F 876547!, F 894168!, F [fragm.] 609130!, G [G photo 8472 at WIS!], P!).

Nomenclatural note.—The herein selected lectotype of *Capparis scabrida* housed at P, has a label with a correct origin of the specimen, "in America equatoriale," and the number "19" added. The B isolectotype of *Capparis scabrida* consist of a branch with a terminal inflorescence, with the two leaves, one inflorescence, and floral pieces detached and remounted. That isolectotype, originally only identified as *Capparis*, was named *Capparis speciosa* (a Willdenow's *nomen nudum*, non *Capparis speciosa* Griseb. [1879], = *Anisocapparis speciosa* [Griseb.] X. Cornejo & H.H. Iltis), as reads the label which is at the upper left corner of the photo 9478, now in a separate sheet (B-W 10055 -00 0). That label has the following handwritten information: "Polyandria Monoginia *Capparis speciosa* racemi(?) terminali, foliis ovato-lanceolatis obtusis mucronatis supra nitidis glabris subtus tomentosis foliola elliptica. Habitat in America meridionali." The discussed isolectotype later was correctly identified by Eichler himself, in a handwritten label of determination, which reads: "*Capparis (Colicodedron) scabrida* H.B.K."

Multi-branched shrubs to trees, to 10 m and 25 cm dbh, erect to low and widely spreading; the stem when injured produces a gum (*Little 6725*); terminal branches complanate or ± tetragonal, densely stellate throughout. Leaves spirally-alternate, few times opposite-decussate, petioles 8–30 mm, lacking pulvini; blade coriaceous (rigidly coriaceous when dry), lanceolate to oblong, (6–)8–23 × 2–7 cm, acute to rounded, sometimes emarginate, apiculate at apex, cuneate to rounded, sometimes retuse at base, olive green (alive), but drying to a bright sulfur-yellow in herbarium material, thinly stellate-tomentose when young, soon glabrescent and smooth or scabrous above, pale grayish or "ashen" greenish-yellow and densely pale stellate-tomentose with a prominent midvein beneath; (7–)12–23 lateral nerves on each side of the midvein. Inflorescences simple, densely corymbose racemes, solitary and terminal or lateral in the axils of leaves, or branched, terminal racemes compounded into complex, stout, (sub)erect, corymbose panicles, to 30 cm, densely stellate, each raceme with only 1–4 open flowers at its end at one time. Floral bracts filiform, 5–12 mm, soon deciduous. Pedicels 2.5–4 cm, densely brown stellate and sparsely dendroid. Flowers dark brown to greenish-brown, densely stellate. Flowers asymmetrical, in perfect flowers the androgynophore-gynophore off-centered within the calyx cup, arching out and upward. Sepal lobes broadly ovate to lanceolate, 10–15 × 5–8 mm, at anthesis cucullate-ascending, acute at the apex, densely brown stellate on both sides, eventually caducous, broadly inserted on the rim of a wide bowl-shaped calyx cup, 9–13 × 6–8 mm, with a 3-lobed nectary cup coating the hypanthium within. Petals narrowly to broadly ovate, oblong or elliptic, 15–23 × 10–15 mm, reflexed and outrolled at the tip at anthesis, widely cuneate to truncate at the sessile base, obtuse to rounded at the apex, white to cream or yellowish, sometimes greenish, stellate on both sides. Stamens 24 to 35, borne in a ring on top of the short 2–3 mm androgynophore, filaments (3.5–)5–7(–8) cm, stellate and dendroid, adnate to each other for 0.5–2 mm at the base; anthers 3–4 mm, white (alive). Gynophore 5–8 cm, creamish-white, maturing to purple (alive), sparsely stellate; ovary ovoid to ellipsoid, 4–6 × 3–5 mm, densely stellate; stigma truncate, sessile. Infructescences with gynophores 7–10 × 0.4–0.6 cm, pedicels 2.5–3.5(–4) cm. Pseudoamphisarcum oblongoid, ovoid, or ellipsoid, slightly asymmetrical, 8–15 × 5–9

cm, pendulous, ± umbonate at the apex, densely stellate, when mature exhibiting 8 longitudinal ± sulcate (dried) lines (usually 4 major, indicating the valves); fruit wall fibrous, 6–10 mm thick, pulp bright orange at maturity, insipid; seeds 15 to 60, subspherical-reniform, often strongly beveled, ca. 1–2 × 1–1.5 cm, surrounded by a densely orange sarcotesta infiltrated by many hairs from the crustaceous reddish-brown testa; embryo yellow.

The amphisarcum is a simple, indehiscent fruit, provided with a thick, woody to subwoody fruit-wall, which retains the shape upon removal of sarcocarp, and never splits in valves after maturity (Spjut 1994: 23, 37). In *Colicodendron scabridum*, the fruits at maturity fall on the ground to eventually decompose and release the seeds, leaving usually four thickly-subwoody, elliptical, abaxially convex, unattached, persistent valves. That fruit type of *Colicodendron scabridum*, which doesn't fit in any of the fruit types known (Spjut 1994), is herein proposed as Pseudoamphisarcum (pseudo + amphisarcum) X. Cornejo (mod. nov.), which means a false amphisarcum.

Local names.—ECUADOR: Sapote (Spanish, *Little 6725*), sapote de campo (Spanish, Van den Eynden et al. 1999: 42), sapote de perro (Spanish, *Cornejo & Bonifaz 7583*), sapote gomoso (Spanish, *Steyermark 54842*); Zapotillo (Spanish, *Brandbyge 42789*); Zapote de perro (Spanish, *Acosta-Solis 8521, Mille 1940, Madsen 64103*). PERU: Sapote (Spanish, *Díaz & Baldeón 2374*), sapote de perro (Spanish, *Woytkowski 5672*). Zapote (Spanish, *Vargas 42*), Zapotillo (Spanish, *Simpson & Schunke 567*).

The bright orange color of the mature fruit pulp of *Colicodendron scabridum* strongly resembles the color of the pulp of a locally (in Ecuador) well known edible fruit called "Sapote" (*Quararibea cordata* [Bonpl.] Vischer, Bombacaceae). This is the origin for the several similar and derived local names of *Colicodendron scabridum*.

"Sapote de perro," one of the local names, refers to *Pseudalopex sechurae* Thomas. This is an endemic canid locally known as "Perro de monte" (Spanish) or "Sechura fox" (English), that has a distributional pattern similar to that of *Colicodendron scabridum* in the dry coastal areas of Ecuador and Peru. When the food is really scarce, the *Pseudalopex sechurae* facultatively eats the fruits of *Colicodendron scabridum* (Bruning 1985; Cornejo 2005).

Zapotillo (Spanish), a town located in a dry forest at the Province of Loja in Southwestern Ecuador, owes its name to the local name of the locally well known *Colicodendron scabridum*.

Phenology.—Flowering mostly between February to October, fruiting mostly September to December. A single tree 4–6 m high, produces 20 to 60 flowers at anthesis per night. Within the nectary cup, three droplets of nectar start to be produced at 19:00 h., each droplet from below of each nectary lobe. By 19:30 h, the nectary cup is full of nectar. But by the next morning at 6:00 h, the flowers don't have nectar anymore, perhaps due to the intense bat activity during the night. The nectar is secreted during one night per flower only. The flowers live one night only and don't produce any scent (Cornejo field obs. in Bahía de Caráquez, Ecuador, July 2004).

Cytology.—$n = 8$ [!Pazy, ECUADOR. Manabí: *Iltis and Iltis 243* WIS, Iltis unpublished ms).

Distribution.—*Colicodendron scabridum* is a characteristic floristic element of dry to very dry or xerophytic areas of western Ecuador and Perú, where is a dune former. This species ranges from sea level in Ecuador from the Province of Manabí, to ca. 2500 m in the mountains of the Province Loja, and in Perú south to Dept. Ancash (Fig. 7).

Ecological interactions and field observations.—The flowers of *Colicodendron scabridum* are visited by the common domestic honey bee, *Apis mellifera* L. Dozens of buzzing bees can be heard from under a tree when the nocturnal flowers are just about to open. The honey bee's activity peaks in and around the flowers of *Colicodendron scabridum* is between 18:30 to 19:30 h. The domestic bees re-start re-visiting the flowers the next morning, as well between 6:00 to 8:00 h. Nocturnal, presumably pollen predator bees such as Halictidae (*Megalopta*?), also visit the flowers at 19:00 h. While both species of bees touch the anthers and the ovaries, it seems however that the true pollinators are bats. From 20:00 to 5:50 h, many small bats frequent the flowers of *Colicodendron scabridum*, which are exposed on long peduncles high above the foliage. The bats beat their wings hovering in the air while licking the nectar from each flower during less than one second,

as hummingbirds are apt to do. The bats do not hold themselves from the flowers as happens to the African Bignoniaceae, *Kigelia africana* [Lam.] Benth. (seen in Bahía de Caráquez, Ecuador, the same locality where *Colicodendron scabridum* was studied by the senior author). When leaving the flower, the bat shakes the inflorescence, presumably helping pollination. It is interesting to note that only the individuals of *Colicodendron scabridum* growing in total darkness are visited by bats. These conspicuously have a higher fruit productivity per tree than the remaining individuals located around the nocturnal lights along the roadsides in the same locality. Additionally, the flowers of *Colicodendron scabridum* are also visited by *Amazilia amazilia*, a hummingbird who visits the old (previous night's) flowers between 7:00 to 8:00 h, and the new flowers just about to open at ca. 18:00 h. Finally, the flowers of *Colicodendron scabridum* are commonly visited by wasps, coleoptera and several species of ants (Cornejo field obs. in Bahía de Caráquez, Ecuador, July 2004).

Uses.—The fruits have been reported as edible for humans and as medicinal against colds and coughs. They are commonly eaten by cattle and donkeys (*C. Cerón et al. 22424*, Van den Eynden et al. 1999: 42, Cornejo field obs.), while the wood is used for fuel and to make handicrafts (*Cornejo & Bonifaz 7583*, Van den Eynden et al. 1999: 42). Finally, a "glue" for paper can be obtained from the cut, gum-oozing ends of the stems (*Cerón 11876*).

Conservation biology.—A characteristic common species in the dry landscape, it does not appear to be in danger of extinction.

Specimens studied. **ECUADOR. Manabí:** Bahía de Caráquez, 6 Jun 1955, *E. Asplund 16569* (S); 10 m, Apr 1944, *M. Acosta-Solís 8521* (F); km 8 carr. Bahía-Tosagua, Universidad Católica, bosque muy seco–seco tropical, intervenido, 80°32'W 00°45'S, 30 m, 31 Oct 1997, *X. Cornejo & C. Bonifaz 5852* (AAU, GB, GUAY, WIS [voucher for DNA]); 20 km carr. a Chone, monte espinoso tropical, 80°25'W 00°38'S, 100 m, 4 Jun 1989, *C. Cerón et al. 6174* (MO, QAP, QCNE, WIS); frente a la Isla Corazón, 80°22'W 00°40'S, ca. 190 m, 18 Feb 1994, *X. Cornejo & C. Bonifaz 1739* (GUAY). 1 km NW of San Vicente, ca. 10 m, 9–12 Jul 1977, *H.H. Iltis & M. Iltis E-228* (WIS); Cantón Sucre, 21–22 km S of Leonidas Plaza, 80°25'W 0°46'S, ca. 100 m, 16 Sep 1993, *G. Webster et al. 30666* (DAV, QCNE); Moteles la Playa, deciduous thorn scrub vegetation, ca. 10 m, 9 Jul 1977, *H.H. Iltis & M. Iltis E-182* (WIS). 10 km SE of Bahía de Caráquez, at km 11–14 along road to Chone near the highest point, ca. 150 m, 8 Jul 1977, *H.H. Iltis & M. Iltis E-243* (B, QCA, WIS [2]); Ad El Recreo, ca. 100 m, 1897, *Eggers 15528* (F, PR). Entre La Salina y Chone, 26 Jul 1945, *M. Acosta-Solís 10638* (F); 1 km N of Portoviejo on main road; hill overlooking town, common on dry coastal hills, 7 Aug 1980, *B. Hansen et al. 7980* (AAU, RSA, SEL, USF, WIS); Portoviejo–Jipijapa road, ca. 1 km S of La Pila, grazed deciduous forest, ca. 200 m, 4 May 1985, *G. Harling & L. Andersson 24821* (GB, QCA, WIS); Jipijapa, 80°35'W 1°21'S, 30 m, 25 Mar 1981, *B. Sparre 20020* (GH, S); 10 km N of Montecristi, 180 m, 29 Dec 1961, *C. Dodson & Thien 1786* (MO, WIS); 11 km W of Puebloviejo, 22 km E of Manta, extremely dry scrub with large bombacaceous trees, ca. 100 m, 28 Oct 1974, *A. Gentry et al. 12203* (MO, WIS); 14 km SW of Manta on new road to San Lorenzo, 80°47'W 1°01'S, 300 m, 2 Jun 1997, *D. Neill & M. Asanza 10706* (MO, QCNE, WIS); between Puerto López and Machalilla, 80°48'W 1°32'S, 70 m, 29 Sep 1984, *J. Brandbyge 42789* (AAU, MO, NY, QCA); Parque Nacional Machalilla, Norte de Puerto López, monte espinoso Tropical, 80°48'W 1°31'S, 70 m, 3 Apr 1994, *X. Cornejo & C. Bonifaz 2326* (GUAY, WIS); comuna Agua Blanca, 80°42'W 1°35'S, 30 m, 7 Jan 1994, *X. Cornejo & C. Bonifaz 1147* (GUAY, QCNE); ibidem, 350 m, 21 May 1995, *X. Cornejo & C. Bonifaz 3900* (GUAY); 80°44'W 1°31'S, 125 m, 2 Aug 1990, *C. Cerón et al. 11671* (MO, QCNE, WIS); 25 Jun 1993, Salaite, Cerro Viejo y punta de Las Sillas, *C. Cerón et al. 22424* (QAP); Joa hacia Mero Seco, desvío a la derecha del cerro La Jacinta y de ahí hasta el cerro Las Colembras, 80°41'W 1°25'S, ca. 420 m, 6 Sep 1991, *C. Josse 638* (AAU, QCA); camino a la Playa de Los Frailes, ca. 25 m, 29 Jul 1992, *M. Gavilánez et al. 966* (NY, QCA, QCNE [2]); Playa Los Frailes, ca. 2 m, 23 Jan 1991, *A. Gentry & C. Josse 72703* (MO, QCNE); Río Blanco–Vuelta Larga, 80°47'W 01°29'S, 150 m, Sep 1986, *C. Bonifaz 1076* (GUAY); Bosque seco aledaño al Parque Nacional Machalilla, 100 m, 25 Nov 1990, *P. Mena & M. García 87* (NY, QCA, WIS); Estero Seco, bosque muy seco tropical, 80°37'W 01°39'S, 150 m, 29 Nov 1993, *X. Cornejo & C. Bonifaz 924* (GUAY); without locality, 80°32'W 0°04'S, ca. 200 m, 9 Jul 1978, *G. Webster 2262* (MO). **Guayas:** Between Daule and Lomas, 9 Oct 1952, *F. Fagerlind & G. Wibom 501* (LD, MO, S); "Prope Guayaquil," Mar 1865, *R. Spruce 4403* (K); Ad Bahía et prope Guayaquil, Apr 1942, *L. Mille 1940* (US); Guayaquil–Playas, Feb 1965, *G. Sánchez 1* (GUAY, WIS); Casas viejas, 22 km W of Guayaquil on road to Salinas, ca. 60 m, 25 Sep 1981, *C. Dodson & P. Dodson 11508* (SEL); El Azúcar, bosque muy seco tropical, 10 m, 19 Jul 2002, *X. Cornejo & C. Bonifaz 7583* (AAU, GUAY, WIS); between Progreso and Playas, ca. 30 m, 27 Oct 1958, *G. Harling 3096* (S); 10 km W of Progreso, ca. 20 m, 29 Oct 1958, *G. Harling 3100* (S); along road between Progreso and Baños San Vicente, 16 Apr 1941, *H. K. Svenson 11501* (BKL); above Palmar on coast north to Santa Elena, 50 m, 13 Mar 1982, *C. Dodson & P. Dodson 12943* (QCNE, SEL, WIS); Cerca a Playa Rosada, ca. 1 m, Jul 1993, *X. Cornejo & C. Bonifaz 275* (GUAY, WIS); Chanduy, "in litore Maris Pacifi," *R. Spruce 6403* (BM, CGE, K); E of Ancón, 20 Sep 1952, *F. Fagerlind & G. Wibom 220* (S); Muey, May 1978, *F. Valverde 23* (GUAY, MO, SEL); Island of Puná, 24 Aug–8 Sep 1836 [voyage of H.M.S. Sulphur], *G. W. Barclay 422* (BM, NY, WIS); Aug 1847, *B. C. Seeman 915* (K); "Insula Puná," Oct 1892, *H. Eggers 14735* (GH, K, LE, M, US); ibidem, 1852, *Andersson s.n.* (S); Isla Puná, path from Puná Vieja to Campo alegre, 80°08'W 02°49'S, ca. 50 m, 4 Nov 1987, *J. Madsen 64103* (AAU); path Río Hondo to Cerro Yanzún, 80°03'W 02°44'S, 50 m, 2 Oct 1987, *J. Madsen 63987* (AAU[2], QCA, QCNE). **El Oro:** Parroquia San Antonio, Hcda. Montecarlo, 22 Mar 1967, *C. Pineda 89* (GUAY, MO, S); entre Arenillas y Puerto Pitahaya, Dec 1978, *L. Albert de Escobar 913* (QCA, WIS); camino entre Puerto Pitahaya y Arenillas, 15 Apr–15 May 1979, *L. Albert de Escobar 1248* (NY, QCA, WIS); at Arenillas, 6 km S, 25 Jun 1943, *E. Little 6725*

(NY, US); 2 km S de Chacras cerca de la entrada a Balsalito en la carretera de la Reserva Militar de Arenillas, suelo Paleustalf, rojo con profundidad variable, 80°14'W, 3°33'S, 200 m, 16 Feb 1997, *H. Vargas et al. 1158* (WIS); ca. 1 km N of Huaquillas, 1 May 1980, *G. Harling & L. Andersson 18813* (GB, WIS); Huaquillas, dry thorn scrub forest, 80°13'W 3°27'S, 5 m, 7 Apr 1980, *L. Holm-Nielsen 22842* (AAU). **Loja:** Cantón Saraguro, caserío Chayasapa, 79°12'W 4°17'S, 2500 m, 5 Sep 1990, *C. Cerón 11876* (MO, QAP, QCNE, WIS); 10 km N El Empalme on Macará–Celica road, 800 m, 12 Feb 1991, *Kessler 2463* (AAU); Rd. Macará–Loja, 16 km S of Catamayo, 79°23'W 4°05'S, 1400 m, 13 Feb 1987, *J. Bohlin et al. 1331* (GB, QCA); between Loja and Portovelo, 3–6 Oct 1918, *J. Rose et al. 23327* (NY, US); El Saucillo, Las Casas Viejas, 80°11'20"W 4°15'40"S, 360 m, 15 Feb 1996, *Van den Eynden et al. 615* (LOJA, QCNE); above Catamayo towards Loja, very dry slope, ca. 1650 m, 9 Oct 1955, *E. Asplund 18077* (B, K, LD, NY, S); between El Tambo and La Toma, 1000–2200 m, 3 Sep 1923, *A. Hitchcock 21330* (GH, NY, US); carr. La Toma–El Tambo, monte espinoso premontano, 79°25'W 4°02'S, 1500 m, 26 Dec 1991 (fr), *D. Rubio et al. 2287* (MO, QCNE, WIS); between Gonzanamá y La Toma, 1400 m, 21–23 Jul 1959, *G. Harling 6065* (S); Catamayo, 1 km SE de La Toma, 79°22'W 4°00'S, 1500 m, 6 Sep 1994, *E. Little et al. 252* (NY, QCNE, WIS); Cerca a Catamayo, 79°21'W 4°00'S, 1238 m, 22 Mar 1994, *X. Cornejo & C. Bonifaz 2148* (AAU, GUAY, QCNE, WIS); Rd. Catamayo–La Toma, ca. 1500 m, 24 Apr 1980, *G. Harling & L. Andersson 18600* (AAU, GB); dry rocky desert hills above La Toma, ca. 1675 m, 24 Oct 1943, *J. Steyermark 54842* (GH, NY); Catamayo valley, *Lehmann 4939* (F, K, LE); along the Río Guayaba, 4800 ft, 8 Oct 1944, *W. H. Camp E-651* (NY, WIS[2]); Río Guayabas, 5 km NW of Catamayo (La Toma), 1300 m, 10 Feb 1945, *F. Fosberg & M. Giler 22933, 22934* (WIS); E side of Catamayo valley, 3 km E of Catamayo, 1690 m, 10 Feb 1945, *F. Fosberg & M. Giler 22927* (WIS); near la Toma, 79°04'30"W 4°00'00"S, 1300 m, 20 Oct 1965, *D. Knight 439* (LE, WIS); ibidem 14 Feb 1965, *D. Knight 609* (WIS); La Toma, 1400 m, *R. Espinoza 537* (F, NY); SW Catamayo, valley along Río Catamayo, 79°21'W 3°59'S, 1355 m, 10 Jul 1989, *L. Dorr & I. Valdespino 6584* (NY, QCA, QCNE, WIS); La Toma-El Tambo, km 5–11 (along gravel roads), vic. Río Catamayo, dry rocks with cacti, 79°21'W 04°03'S, 1300–1500 m, 15 Oct 2000, *J. Madsen & J. Gálvez 7441* (AAU, NY); Rd. San Pedro de La Bendita–Catamayo, km 6.5 (4 km from Catamayo), 79°23'W 3°57'S, ca. 1325 m, 16 Jul 1996, *G. P. Lewis et al. 2451* (K, LOJA, QCNE); Cerro Villonaco, 1800 m, 13 Feb 1985, *G. Harling & L. Andersson 22023* (GB, NY, QCA, WIS). **PERU. Tumbes:** Prov. Tumbes, Dtto. Pampas del Hospital, Huapalas, 100m, 26 Jun 1964, *J. Vargas 42* (NY); Dtto. San Juan de la Virgen, along Quebrada Las Peñas, betw. San Juan de la Virgen and Matapalo, 6 Jan 1968, *D. Simpson & J. Schunke 567* (F, NY). **Piura:** Prov. Piura, Piura, 1928, *O. Haught F-69* (F); Prov. Paita, Paita, *D'Urville (Lesson?) s.n.*, 1825 (B [2]); 25 Jun 1914, *Mr. & Mrs. J.N. Rose 18513* (NY); ibidem, 25 Jul 1901, *R. Williams 2927, 2928* (NY); Prov. Sullana, Sullana, 260 m, 16 Apr 1987, *C. Díaz & S. Baldeón 2374* (MO). **Lambayeque:** Lambayeque, 1150 m, 8 Jan 1964, *P. Hutchinson & J. Wright 3518* (MO); Lambayeque, km 698 betw. Lima and Sullana, chief dune former in desert, sea level, 5 Oct 1959, *B. Maguire & C. Maguire 44389* (F, MO, NY). **Cajamarca:** Prov. Celendín, Balsas-Celendín rd., 1–5 km from Balzas, 78°04W 6°50'S, 910–1160 m, desert slopes, Río Marañon Valley, 23 Feb 1984, *D. Smith 6145* (MO, NY); Río Marañón Valley, Celendín-Balsas rd. 25 km and onward from Celendín, 78°05'W 06°51'S, 1000–2500 m, 16 Jul 1983, *D. Smith & I. Sánchez 4330* (MO, NY); Prov. San Ignacio, San Ignacio, 600–700 m, 78°46'W 5°12'S, 16 Apr 1996, *J. Campos y P. Díaz 2615* (MO). **La Libertad:** Prov. Trujillo, Trujillo, 15 Apr 1988, *C. Díaz & S. Baldeón 2784* (MO); Cerro Campana, 800 m, 25 Oct 1983, *A. Sagástegui 10965* (MO); ibidem, 100 m, 14 Jul 1973, *A. López & E. Araujo 7978* (MO, NY); banda occidental, 215 m, 10 Sep 1949, *N. Angulo 1250* (NY); base del Cerro Campana, 60 m, 23 Oct 1983, *A. Sagástegui s.n.* (NY); in quebrada bottom on SE side of Cerro Campana, 150–200 m, 24 Sep 1957, *P. Hutchinson 1358* (NY); Prov. Pacasmayo, Pacasmayo, 79°24'W 7°33'S, 120 m, 13 Jul 1983, *D. Smith 4221* (MO); just S of San Pedro de Lloc, 100 m, 31 Dec 1963, *P. Hutchinson & J. Wright 3352* (F, G, GH, HEID, K, LE, MO, MICH, M, NY, P, S, US, USM); ca. 96 km N of Trujillo on Panamerican hwy, coastal desert dunes, 60 m, 16 Oct 1984, *M. Dillon & M. Whalen 4014* (F, MO); 84 km N of Trujillo, 3 Mar 1973, *A. Richardson 2029* (NY). **Ancash:** 78°06'W 10°11'S, 11 Oct 1958, *K. Rahn 318* (MO, ex Tropicos).

3. Colicodendron valerabellum H.H. Iltis, T. Ruiz & G.S. Bunting, sp. nov. (**Figs. 2–7**). TYPE: VENEZUELA: Edo. Trujillo, Distr. Valera, "Arbusto de 3 m de alto; hojas brillantes por el haz, envés con pubescencia estrellada de color amarillo y caediza al tacto. Pedúnculo de la inflorescencia secundaria castaño claro e inclinado con respecto al eje caulinar. Botones con néctar. Sépalos castaño oscuro, ásperos al tacto; pétalos color crema. Estambres en número de 64, sobre un corto androginóforo, gineceo gris oscuro y atrofiado en las flores masculinas examinadas. La inflorescencia con hormigas y 'pegones' [Himenopteros]." Se observaron 17 individuos en un área de 3 m^2 [3 km^2?]," Carretera vieja Valera-Motatán, saliendo de Valera por el barrio La Floresta. Selva decidua muy intervenida, 550 m, 70°36'W 9°20'N, 16 Mar 1991 (fl, y fr), *T. Ruiz-Zapata & C. Benítez de Rojas 4671* (HOLOTYPE: MY; ISOTYPES: K, MO, US, VEN, WIS; photocopies together with individual leaves F, IRBR, MER, NY, PORT, S, UC.).

Colicodendrum species novum cum pubescentia stellata, calyx valvatis 1-seriatis cum nectarius cupularibus et fructus pachycarpus, affinis *Colicodendrum yco* Mart., a qua differt frutex vel arbusculis pauciramosis cum foliis subverticillatis (nec ramosissimis cum foliis oppositiis), inflorescentiis racemosiis (nec paniculatiis), staminis (35–)50–64(–70) (nec 14 ad 20), gynophoriis ca. 8–9 cm longiis, (nec gynophoriis 3.5–5 cm longiis), et fructis subglobosis (nec ellipsoidiis).

Evergreen palmoid treelets [or in damaged plants with one or two additional unbranched stems from near the base, some of these decumbent and sending forth 1 to 3, erect, leaf- and sometimes flower-bearing lateral-horizontal shoots], to 5 m long and 3–5 cm dbh often crowded (colonal?); young branch(es) dark-brown echinate or echinate-stellate; stipules absent. Leaves subsessile to short-petiolate, to 1.5 cm, grouped in crowded whorls at the end of the terminal branches exposing mostly leafless internodes, nodes of leaf insertions ca. 3–6 cm, swollen, blades oblanceolate to narrowly elliptic, (16–)20–50 × 4–9 cm, stiffly coriaceous

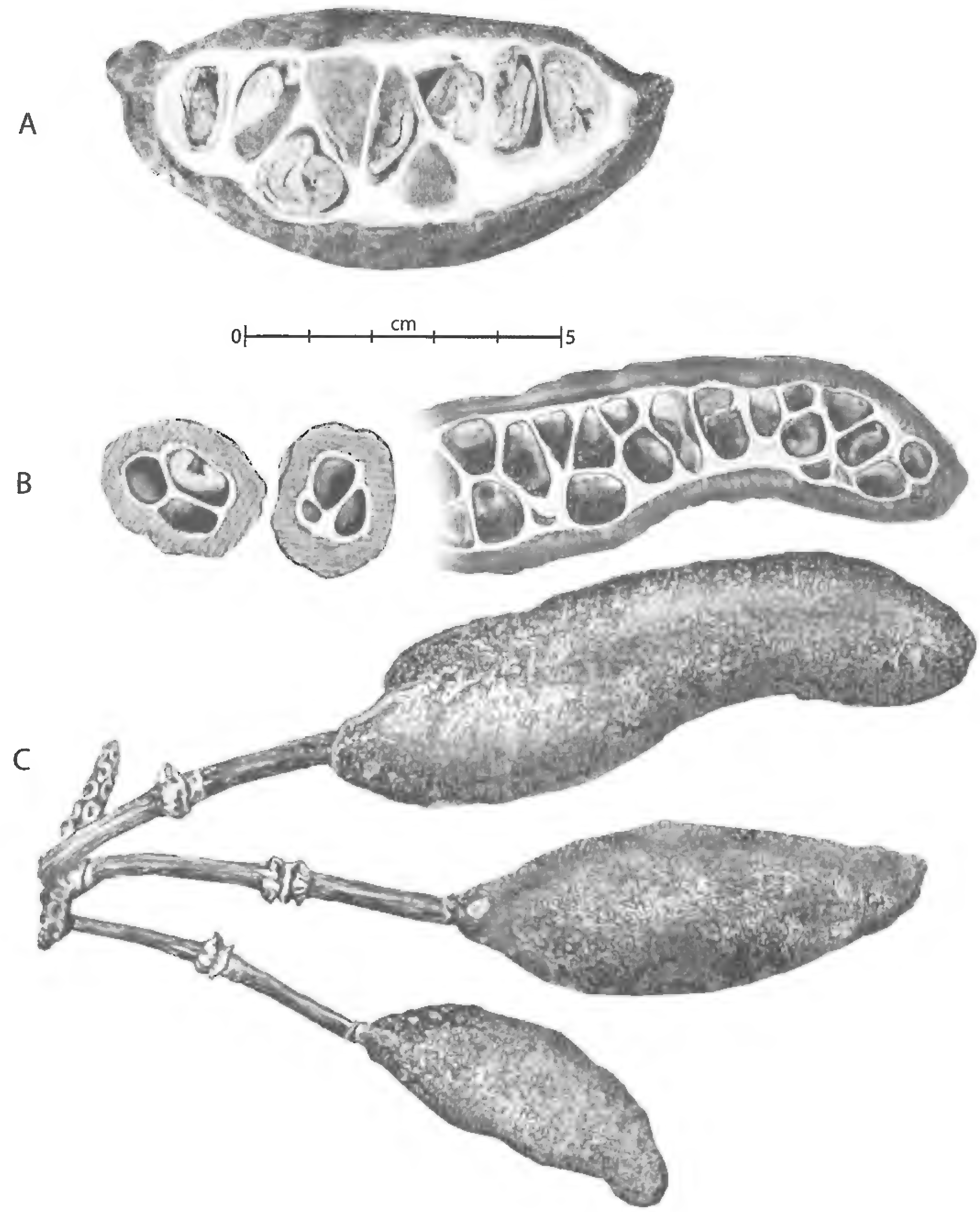

Fig. 2. ***Colicodendron bahianum*** **X. Cornejo & H.H. Iltis. A. Longitudinal section of a mature fruit. B. Transversal and longitudinal sections of inmmature fruits. C. Infructescence. (A.** ***Hatschbach & Motta 63068*****, US. B–C.** ***de Mello Filho 2988*****, CEPEC).**

and hard but somewhat flexible (alive), chartaceous (dry), attenuate but rounded-retuse to subcordate at the base, acuminate or acute to widely obtuse at the apex, margin inconspicuosly thickened and revolute, lustrous green (alive) with a impressed to sulcate midvein, prominently and coarsely rugose (i.e., bullate), with the blade surface between the deeply impressed midrib and main nerves prominently convex and smooth, ap-

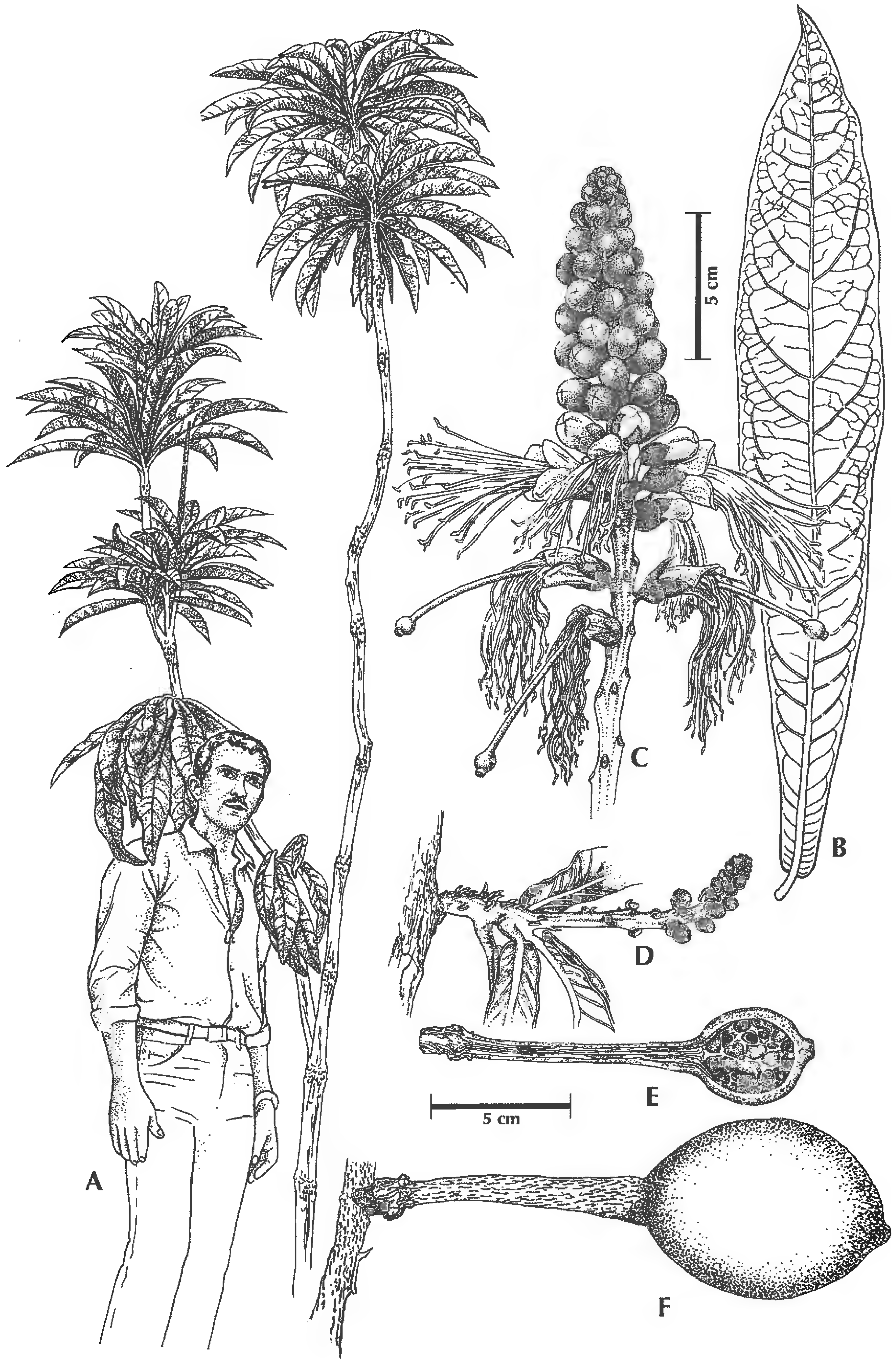

Fig. 3. *Colicodendron valerabellum* H.H. Iltis, T. Ruiz & G.S. Bunting. **A.** Habit. **B.** A leaf blade. **C.** An inflorescence with three hermaphrodite flowers in postanthesis at base; four male flowers above them in full bloom and three beginning to wilt; and, above these, some 50 male flower buds. **D.** An inflorescence bearing (sub)sessil flowerbuds. **E–F.** Immature fruit. (A. After photo of *Bunting & Trujillo 13120*. B–D. *Iltis et al. 30547*, WIS. E–F. *Ruiz & Villafañe 4764*, MY). A–E, drawings by Marian Firmani; F, by T. Ruiz Z.

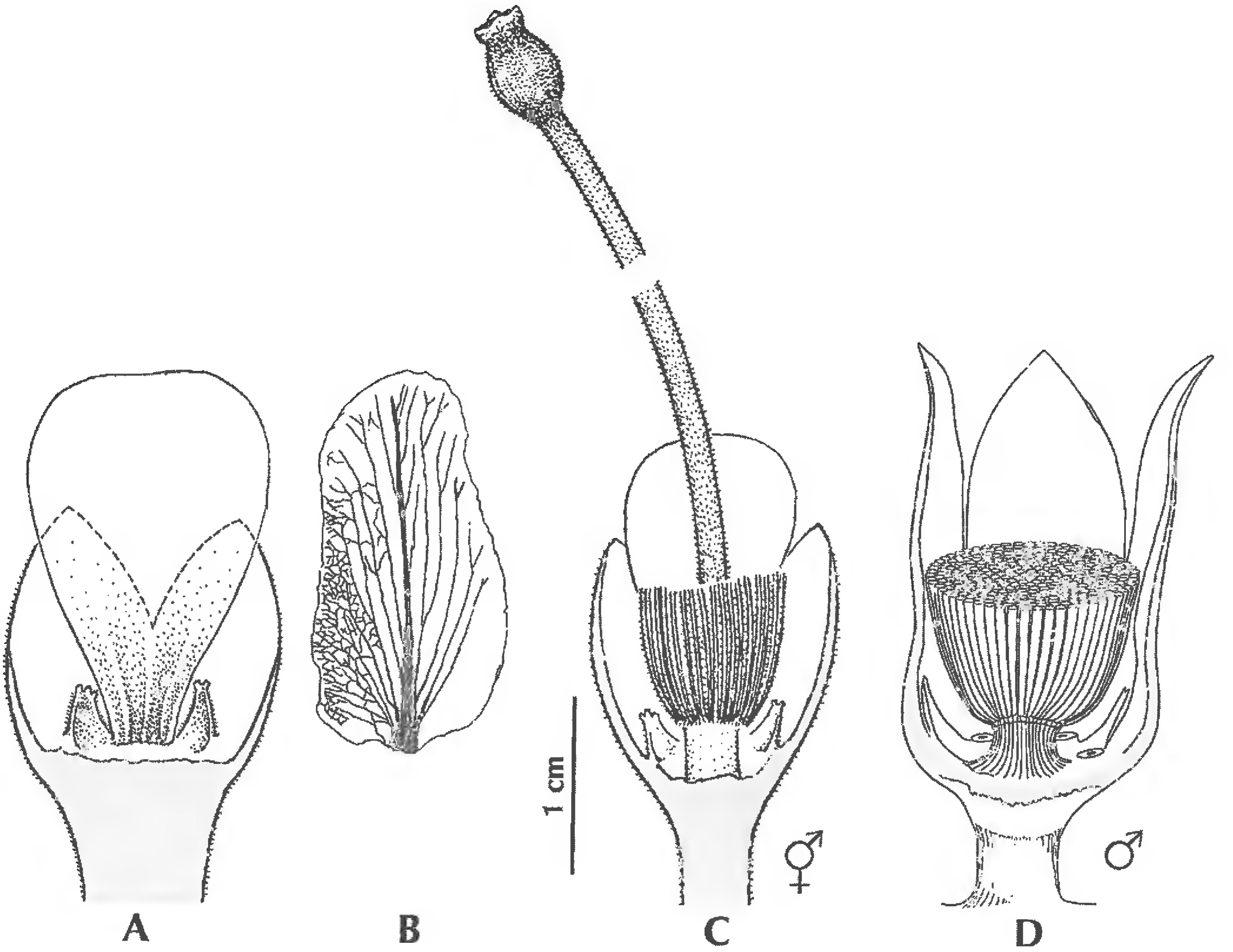

Fig. 4. *Colicodendron valerabellum* H.H. Iltis, T. Ruiz & G.S. Bunting. A. Schematic section of flower, showing calyx in relation to one petal and the alternating scaly nectary appendages. B. Petal, with its detailed nervature shown only in lower left area. C. Hermaphrodite flower, showing columnar androgynophore arising from the nectary dish, cut-off bases of staminal filaments, and abbreviated gynophore tipped by a young ovary. D. Male flower, showing scaly nectary appendages, three petal bases and phalanx of stamens touching petals and sepals to create an inner nectar chamber. (A–D. *Iltis et al. 30547*). A, C by Manara; B, D by Iltis.

parently glabrous (glabrescent) above; paler green (alive) and with a strongly prominent midvein and densely stellate beneath; 14 to 26 pairs of lateral nerves. Inflorescences terminal, racemose spike, stiffly erect and densely coarsely echinate-stellate throughout, rough to the touch, arising from the center of a leaf whorl, axis eventually elongating to 40 cm (or more?) × 6–10 mm tick, stout, bearing 20 to 100 or more subsessile, rusty-brown (alive) flower buds, but only 2 to 5 flowers opening each night in successive acropetal circles. Floral bracts subulate, ca. 5–7 mm, deciduous, densely brown-echinate. Pedicels 2–3 × 3–4.5 mm. Sepals ovate to lanceolate, 15–25 × 8–12 mm, ± acute at apex, densely yellow-brown (alive) echinate abaxially; hypanthium ca. 2–3 mm depth, coated by a 4-dentate nectary dish within, nectary appendages deltoid, ca. 3–4 × 3–4 mm, emarginated to bifid at the apex. Petals apparently inserted at the edge of the nectary cup, at anthesis obovate to obovate-oblong, 25–32 × 10–15 mm, widely obtuse to truncate at apex, longitudinally nerved, bright yellowish or cream (alive), densely pale-brown echinate-stellate abaxially. Stamens (35–)50–64 (–70), filaments (4–)6–7 cm, stellate at the base, inserted on a expanded torus-like androgynophore, at anthesis projecting forward in a narrow phalanx, anthers 3.8–5 mm. Gynophore 8–9 cm, densely stellate; ovary 6–7 × 4–5 mm, subglobose, 8-ribbed, densely stellate; stigma sessile, truncate, discoid. Infructescences a stout gynophore, ca. 10 mm wide. Amphisarcous subglobose, ca. 9 × 7 cm (immature), subpendulous, apex umbonate with an apically stigmatic depression at the umbo, densely rusty-brown echinate, yellow when

Fig. 5. *Colicodendron valerabellum* H.H. Iltis, T. Ruiz & G.S. Bunting. **A.** Terminal two leaf whorls of unbranched, 4 m tall treelet, showing conduplicate arched leaves and leafless inter-whorl stem segment (Thirza Ruiz Zapata on right, Carmen E. Benítez de Rojas on left). **B.** Lateral secondary shoot, terminating in a small spike. **C.** Enlarged base of spike shown in B, with bract-like processes and base of a petiole. **D.** Pseudoverticil of leaves showing leaf bases. **E.** Pseudoverticil of D, with leaves removed to show crowding of petioles and a densely bracted terminal bud of future replacement stem or inflorescence. (A–D, photos by Iltis of *Iltis et al. 30547*, from near type locality).

Fig. 6. ***Colicodendron valerabellum*** **H.H. Iltis, T. Ruiz & G.S. Bunting. F. Rigid, massive peduncle of primary inflorescence, covered with symmetrically-spaced pedicel scars. G. Terminal pseudoverticil of primary stem, showing base of old, now decomposed peduncle and six branch buds covered with bract-like processes. H. Two immature fruits near base of rigid, stout, erect peduncle. (F–G, photos by Iltis of *Iltis et al. 30547*, from near type locality. H, photo by G. Bunting).**

ripe (fide a local informant, *Iltis et al. 30547*); fruit wall thick, pulp whitish or cream, seeds numerous (ca. 30?), reniform, 20–25 x 13–14 mm (immature), seed coat red-purple (fide Bunting).

Colicodendron valerabellum differs widely from *C. yco* by the characters written in the Latin diagnosis. Due to the leaves arrangement in crowded whorls at the end of the terminal branches (Fig. 3A, 5A) and unbranched inflorescences (Fig. 3C), *Colicodendron valerabellum* seems more closely related to the Brazilian *C. bahianum* (Fig. 1A). However, *Colicodendron valerabellum* differs from the latter by having spicate inflorescences with a larger central axis, 10–30 cm (Fig. 3C, vs. racemose, with shorter central axis, 1–5 cm, Fig. 1A), bearing subsessil (vs. 1.8–4 cm, pedicellate) flowers, longer gynophore, 8–9 cm (vs. 1.6–2 cm), subglobose (vs. oblong) ovaries; subglobose fruits (Fig. 6H, vs. oblong-ellipsoid, Fig. 2) and by its localized distribution, in northwestern Venezuela (vs. eastern Brazil, Fig. 7).

Phenology.—*Colicodendron valerabellum* apparently begins to flower in November, not long after the end of the rainy season, and continues to bloom into April or May (or "does it flower twice a year, once in May and again in November?"), with older hermaphrodite flowers beginning fruit enlargement with the commencement of the rainy season at the beginning of May, forming young fruits by July, "when new growth was just starting," and completing their growth by the following January or February.

The terminal inflorescence of *Colicodendron valerabellum* is apparently an extension of the apical mer-

istem that continues to grow from the center of the upper-most leaf whorl. It is, however, a structure most unusual in many respects, not the least of which is the fact that its flowers are essentially sessile or subsessile on the peduncle axis, with the pedicels very short and thick, so that this structure, rather than a *raceme*, could better be called a *racemose spike*. The remaining species of *Colicodendron* and even of the neotropical Capparaceae s.s. have flowers borne on well developed pedicels. In this comparatively specialized species, this loss of pedicel is linked to a basically primitive, racemose inflorescence, while its three relatives, *C. bahianum*, *C. yco* and *C. scabridum*, have pedicellate flowers in racemes or panicles, presumably the derived condition. Correlated with this loss of pedicel in *C. valerabellum* may be the great length, thickness and stiffness of the peduncle, truly spike-like in the non-botanical meaning of the word, ultimately becoming a full centimeter thick and to 40 cm long, which eventually decompose. Around the stubby remains of the old inflorescence in the center of the leaf whorl, several axillary buds, densely covered with subulate bracts, may be initiated. These in turn may produce 1 to 3 replacement axes, essentially by continuing the unbranched growth upward and the production of another flowering spike, or else lead to the branching of the stem into 2 or 3 axillary branches.

Although variable in particulars among individuals, the primary terminal spikes bear flowers in the following sequence: the lowest floral buds soon abort, leaving only pedicel scars on the peduncle (these buds are usually naked, but in some inflorescences subtended by up to 20 or so small leaves rapidly decreasing in size upward and spaced over a distance of some 10 cm). Moving upward, the next 3 to 6 flower buds, well spaced and the first to burst into bloom, develop into fully functioning hermaphrodites, in which the many stamens are exceeded for about 1 cm by a gynophore bearing its well-developed ovary. Finally, towering above the circle of hermaphrodite flowers, and densely aggregated at first into a narrowly conical inflorescence, are some 20 to 100 staminate flower buds, with only 2–3(–5) of these blooming at one time, beginning at base and continuing upward. The whole inflorescence thus has a long-extended flowering period lasting perhaps a month, and in the process gradually elongating the peduncle to its maximum length. Once the staminate flowers finish blooming, they soon wilt and fall off, leaving only the symmetrically placed, oval pedicel scars on the peduncle.

If the hermaphrodite flowers at the base of the spike become fertilized and commence fruit development, the peduncle above them eventually dries up and eventually decomposes. But if these hermaphrodite flowers are not fertilized, not only do they fall off, but also the peduncle then often retains its stiff, thick structure to eventually produce a new set of hermaphrodite flowers near its tip some 30 cm or more up from its base. This double insurance that seeds will eventually be produced may be the key to understanding the function of so massive a structure.

Clues to the enigmatic reproductive morphology of *Colicodendron valerabellum* must lie in its pollination agents. Of the eight main attributes of the bat pollination syndrome (Chiropterophily) cited by various authors (Pijl 1961: 51; Faegri & Pijl 1966: 114; Vogel 1958: 492), the following six would seem to apply to *Colicodendron valerabellum*: 1) Nocturnal anthesis, the flowers lasting only one night. 2) Flowers and inflorescences strong enough to carry the weight of a bat (subsessile, often many flowers on the strong pedicels, thick calyx, powerful peduncle, i.e., racemose spike axis). 3) Honey abundant, mucilaginous, accessible (to sphingid moths as well). 4) Flower (corolla) yellowish or creamy. 5) Pollen abundant. 6) Inflorescence exposed high above the foliage.

Biological interactions.—According to a local informant, the fruits of *Colicodendron valerabellum* are eaten by deer (*Iltis et al. 30547*, WIS).

Why the big fruits of *Colicodendron valerabellum* should be borne high above the leaves is a curiosity, when in its close relatives, as in most *Capparaceae*, heavy fruits hang down. Or were the fruits/seeds of *Colicodendron valerabellum* dispersed internally by the now extinct megafauna as the giant Gomphotheres (Janzen & Martin 1982), as suggested for *Neocalyptrocalyx muco* (H.H. Iltis, Cumaná, Delgado & Aymard) X. Cornejo & H.H. Iltis, another giant-fruited Capparaceae of northern Venezuela and Colombia? (Iltis et al. 1996: 379, see *Capparis muco*).

Cytology.—Unknown.

Distribution.—*Colicodendron valerabellum* is known only from one limited metapopulation of several, scattered minute populations, with perhaps a total of 20 to 40 plants, growing in extremely disturbed, open tropical deciduous forest remnants and thickets on top of 10–20 m high, steep and badly eroding road cuts and local trash dumps scattered for 3 to 7 km north of Valera (654 m) along and immediately above the *old* highway to Motatán (ca. 500 m), in northwest Venezuela (Fig. 7). Growing in seasonally dry, semi-deciduous to deciduous open forest or woodlands of medium-sized trees, the "bosques higrófilos y mesófilos de las sierras en la región Andina" (Hueck 1960), or in degraded secondary thorn thickets (matorral).

Conservation biology.—*Colicodendron valerabellum* appears to be close to extinction, but with all known populations restricted to the edge of the old yet easily accessible Valera-Motatán highway, and the rest of the landscape barely explored, the possibility exists that the extensive woodlands covering the hills above the road may well hold more extensive stands. In fact, this is also suggested by the presence of a common name, "fruto de venado" (fruit of the deer), since rare species are generally not honored with common names.

The few plants known to exist are certainly in trouble reproductively: except for the inflorescence with two young fruits photographed by Bunting in 1983, the two somewhat older fruits collected by Ruiz-Zapata in 1997, and the five hermaphrodite flowers with developing ovaries at the tip of an inflorescence collected by Ruiz-Zapata in 1998, no other fruits, young or old, have ever been located despite assiduous searching. Perhaps, like many a taxon at the end of its evolutionary career, *C. valerabellum* is not reproducing well. Negative human influences such as firewood gathering, land clearing, and grazing by cattle as well as the unknown but negative impact of pesticide spraying can also not be discounted.

What is clear, in any case, is that the limited fruit production in all the examined populations (by H.H. Iltis) may be due to one or more of the following: 1) The often densely crowded stems may be clones, and, if self-incompatible, cannot form fruit unless cross-pollinated; 2) land clearing may have reduced genetic diversity to the point of no return; 3) the population is inbred, reducing seed production; 4) populations of the pollinating agents (sphingid moths, bats, or hummingbirds) have been much reduced by pesticide application to the local maize fields; 5) the species is adapted to an undisturbed summergreen open woodland periodically cleared by fire, and now these relictual stands have to compete with weeds in a liana-rich, secondary community induced by human disturbance; 6) A remarkable number of Capparoids in the region, have extra-large, more or less woody, indehiscent fruits that, as one of us suggested (Iltis et al. 1996) may have had Gomphotheres, now extinct, as their dispersal agent (Janzen & Martin 1982).

PARATYPES. **VENEZUELA: Edo. Trujillo:** Dtto. Valera, carr. vieja Valera-Motatán, E-facing slopes of Río Motatán Valley, foothills of the Cordillera de Mérida of the Andes, on top of heavily eroding road cuts, 20 m above the old highway from Valera to Motatán, ca. 4 km N of Valera (1.4 km N of entrance to old hwy. from new hwy.), [ca. 70°36'W 9°21'N], 600 m, 10 Jan 1991 (y fl), *H.H. Iltis, T. Ruiz & C. Benítez 30547* (WIS); 7 km N. of Valera (2 km. S of Motatán), *H.H. Iltis et al. 30548* (MO, MY, US, WIS); carr. vieja, en ladera, matorral deciduo, 600 m, 31 Mar 1996 (fl), *T. Ruiz & Villafañe 4740* (MY); alrededores de Valera, en bosque deciduo intervenido por deforestación para conucos [maize fields] y también el uso como basurero, 435 m [?], 10 Jan 1997 (fl., fr), *T. Ruiz & Villafañe 4764* (MY); carr. vieja, en matorral deciduo, 590 m, 31 Jan 1998 (old fl.), *T. Ruiz, Villafañe & Hernández 4801* (MY, WIS), 1 May 1998 (fl), *T. Ruiz, Hernández & Noguera 4802* (MY), carr. vieja, ca. 3 km N de Valera (from the last gas station), en ladera a la izquierda de la vía, en zona de bosque semideciduo ahora alterado, ca. 450 m, 6 Jun 1983 (y fr), *G. Bunting & Trujillo 13120* (WIS); carr. vieja, Agua Viva-Valera 3.5 km debajo de Valera, a la derecha de la vía, 500 m, 28 Nov 1982 (fl), *A. Stoddard s.n.* (MY, NY [2], WIS); carr. Vieja, zona perturbada, 9 May 1980 (fl), *J. Szwarcbort & A. Stoddard 14* (US, VEN).

4. Colicodendron yco Mart., Flora 22, Bleibl. 1:25. 1839. (**Fig. 7**). *Capparis yco* (Mart.) Eichler in Martius, Fl. Bras. 13:272. 1865. TYPE: BRAZIL. BAHIA: Habitat in silvis Catingas ad Caitete, Rio de Contas etc. Provinciae Bah. et ad Malhada ad Salgado usque in P. Min. Ger., Sep–Oct, *C. Martius s.n.* (LECTOTYPE, designated here: M [M photo at WIS!]; ISOLECTOTYPES: BM, K, M).

Capparis speciosa Moric. *nomen nudum* (non *Capparis speciosa* Griseb., 1879), cited in Eichler in Mart., Fl. Bras. 272. 1865. Brazil, Bahia, Serra da Jacobina, 1839 (fl), *J. Blanchet 2564* NY 387633! (from C. Meisner herb.). NOTE: *J. Blanchet 2564* B 10 0242727!, it has been determined by error (by H.H. Iltis 1983) as the isotype of *Capparis yco* Mart..

Many branched shrubs to trees, 2 to 6 m tall; terminal branches complanate, angulate, often ± subtetragonal, densely stellate. Leaves opposite, petioles 0.5–2 cm, lacking pulvini; blades coriaceous, lanceolate to

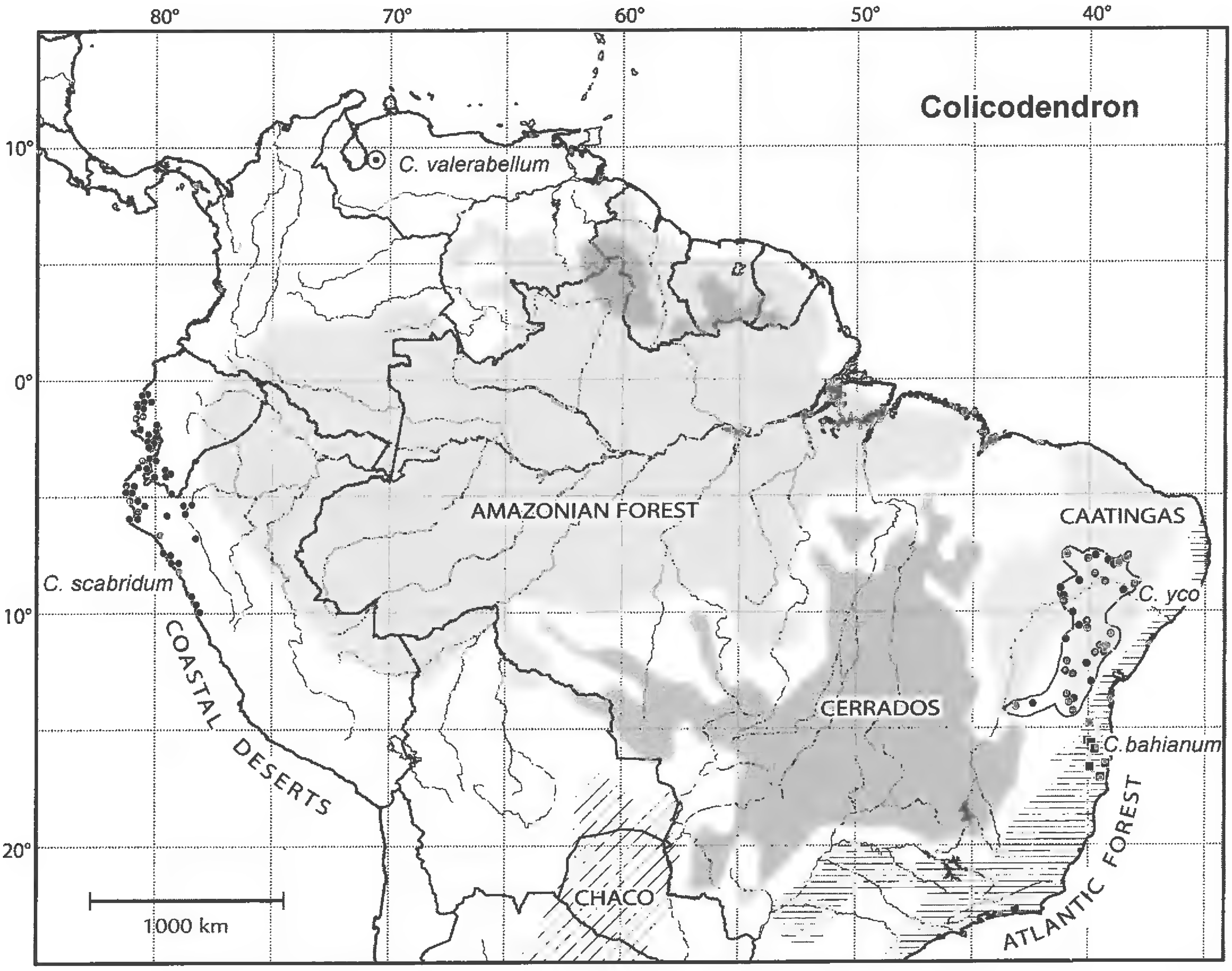

Fig. 7. Distribution of *Colicodendron* Mart. The pronounced morphological differentiation of these four species, disjunct in widely separated regions on the far edges of the Amazon Basin speak for an ancient evolutionary history: 1) *Colicodendron scabridum*: locally common, ranging from the dry-season deciduous, xeric, coastal woodlands near Canoa, Prov. Manabí, Ecuador, south through the dry thorn scrub of coastal Ecuador to the extremely arid deserts of Peru as far as Casma, Prov. Ancash; and inland to the dry, inter-Andine valleys near Loja, Ecuador and the upper Río Marañón, Prov. Amazonas, Perú. 2) *Colicodendron valerabellum* H.H. Iltis, T. Ruiz & G.S. Bunting: A highly local endemic, restricted to a stretch of road ca. 3–6 km north of Valera along the old highway to Motatán, Est. Tujillo, Venezuela, in open to dense but sunny, deciduous to semi-evergreen, tropical, mesophyllous dry forests or ceroid woodlands and thickets, at elevation of ca. 600 m. 3) *Colicodendron yco* Mart.: Widespread in the northeastern Brazilian states of Bahia and Pernambuco (and, barely, Ceara), in the Caatinga, and drought-frequented land, where the vegetation is xerophytic, summer-deciduous, and drought-adapted. 4) *Colicodendron bahianum* X. Cornejo & H.H. Iltis, restricted to moist and wet forests at SE of Bahia State, at Eastern Brazil. (Distribution of *C. yco* in Pernambuco adapted from Costa e Silva 1995).

oblong or oblong-elliptic, 9–25 x 3–8.5 cm, usually retuse to cordate at the base, acute to widely obtuse and apiculate, few times rounded to truncate or notched at the apex, margin entire to sinuate, dark green, glossy (alive) and glabrescent above, whitish, whitish-grey, pale green or pale tan (alive), with prominent nerves and densely stellate beneath; (8–)10–16 pairs of lateral nerves. Inflorescences axillary and terminal, paniculate, rarely solitary axillary flower (*Pinheiro 1453*), densely stellate. Floral bracts linear-subulate, 5–10 mm. Pedicels 1–2 cm, articulated. Sepals 1–1.8 x 4–7 mm, the lobes acute to obtuse at apex, reflexed at anthesis, cream or dull-yellow, densely stellate, deciduous; nectary a 4-dentate cup, the teeth 3–5 x 2–4 mm, triangular, acute. Petals oblanceolate to oblong, 15–30 x 5–7 mm, at anthesis all together erect resembling a tubular corolla, reflexed at the upper third, yellow to orange-yellow, stellate adaxially, densely stellate abaxially. Stamens 14 to 20, filaments 3.5–4 cm, stellate at the base, inserted on a stellate androgynophore, anthers ca. 3–4 mm, yellow (alive). Gynophore 3–5 cm; ovary ovate, 3–5 mm, both densely stellate; stigma

capitate-disciform. Infructescences with gynophores 3–5 cm, pedicels 1–4 cm; amphisarcous ellipsoid, 6–10 x 4–6 cm, subpendulous, apex umbonate with an apically stigmatic depression at the umbo, densely stellate, bearing 10 to 20 seeds, testa light brown, crustaceous, glabrous.

Icones.—*Colicodendron yco* is illustrated in detail in Flora Brasiliensis (Eichler in Mart. 1865, tab. 60, see *Capparis yco*).

Local names.—Icó (Portuguese, *R. Santos & A. Castellanos 24350*), icó branco (Portuguese, *Laurênio et al. 262*), icó de cavalo, icó preto (Portuguese, Costa e Silva 1995: 75).

Biological interactions.—The base of the flower is visited by small ants (*Harley 27133*).

Cytology.—*n* = 8 [!Pazy, BRAZIL. Bahia: *Mori et al. 11218*, WIS, Iltis unpublished ms).

Distribution and ecology.—Widespread in the northeastern Brazilian states of Bahia and Pernambuco (and, barely, Ceara), in the Caatinga, a semi-arid (300–800 mm/year rainfall), hot (23°–28° C yearly average) and drought-frequented land, where the vegetation is xerophytic, summer-deciduous, and drought-adapted (Costa e Silva 1995: 74).

Specimens studied. **BRAZIL. Pernambuco:** Mun. Belém de São Francisco, ilha do Meio, 18 Jul 1967, *E. Tenório 314* (IPA); Mun. Cabrobó, entre Cabrobó e Terra Nova, 15 Apr 1971, *D. Andrade-Lima et al. 767* (IPA); Mun. Inajá, Reserva Biologica de Serra Negra, chapadão arenítico, solo arenoso recoberto por matéria orgânica em decomposição, 15 Sep 1995, *M. Tschá et al. 236* (NY, PEUFR); 16 Sep 1995, *M. Tschá et al. 247* (NY, PEUFR); ibidem, 9 Dec 1995, *A. Laurênio et al. 262* (NY, PEUFR); Mun. Petrolina, Fazenda Santa Maria, proximo a divisa com Santa Maria da Boa Vista, 3 Sep 1968, *G. Carvalho 54* (HST). **Bahia:** Mun. Vitoria da Conquista e Jequié, 26 Sep 1963, *R. Santos & A. Castellanos 24350* (NY); Mun. Jequié, Estrada que liga Jequié a Lafayete Coutinho, ca. 11–17 km a W de Jequié, caatinga herbáceo-arbustiva, 19 Nov 1978, *S. Mori et al. 11207, 11218* (NY); Jequié, 28 Sep 1979, *K. Kubitzi & H. Poppendieck 79-262* (NY); De Jequié para Milagres, 20 Sep 1965, *A. Duarte 9545* (NY, RB); Serra do Castanhão, 14.5 km S of Jequié on BR 116 to paved road (at Churrascaria Corujão), then 7.3 km W of BR 116, 40°11.35'W 13°57'S, arborescent caatinga, 575 m, 19 May 2001, *W. Thomas & S. Sant'Ana 12527* (NY); 40°11.46'W 13°56.52'S, 600 m, high elevation semi-deciduous forest with some caatinga species, 23 Oct 2001, *W. Thomas et al. 12567* (MO, NY); Mun. Juazeiro, N end of Serra da Jacobina at Flamengo, 11 km S of Barrinha (ca. 52 km N of Senhor do Bonfim) at Fazenda Pasto Bom, 42°12'W 10°00'S, Quartz formation and surrounding caatinga, 24 Jan 1993, *W. Thomas et al. 9632* (NY); Serra da Jacobina, 1839, *J. Blanchet 2564* (B, NY); Mun. Rui Barbosa, 8.5 km from Rui Barbosa along right side of old road going via Povoado Alagoas to Itaberaba, dense tall, partly deciduous seasonal forest, 40°23'W 12°15'S, 29 Jan 1993, *J. Kallunki & J. Pirani 392* (NY); Mun. Rio de Contas, 7 km da cidade na Estrada para Livramento do Brumado, 41°50'W 13°38'S, 650 m, Caatinga, 12 Dec 1988, *R. Harley et al. 27133* (MO, NY); Serra do Rio de Contas, by the waterfall of Rio Brumado just N of Livramento Brumado, ca. 41°50'W 13°38'S, ca. 460 m, 20 Jan 1974, *R. Harley et al. 15339* (MO, NY); Mun. Riachao do Jacuipe, ca. 30 km na Estrada de Riachao do Jacuipe para Capim Grosso, caatinga, 14 Mar 1990, *A. de Carvalho & J. Saunders 2765* (CEPEC, NY); Lagoa da Eugenia S end near Camaleão, ca. 10°40'S 39°43'W, 300 m, 21 Feb 1974, *R. Harley 16284* (NY); Quemaidas, 9–11 Jun 1915, *J. Rose & P. Russel 19843, 19871* (NY); 5 km al S de Ichu, camino a Tanquinho, ca. 39°09'W 11°48'S, ca. 300 m, 15 Jan 1997, *Arbo M.M. et al. 7261* (CTES, NY); 30 km N of Serrinha, ca. 39°00'W 11°30'S, 2 Nov 1972, *T. Ratter & Da Fonsêca 2704* (NY[2]); Ba. Maracás x Pouso Alegre km. 27, caatinga, 8 Jul 1971, *R. Pinheiro 1453* (CEPEC, NY); Salgada, 15 May 1918, *H. Curram 277* (GH, NY).

KEY TO THE SPECIES OF *COLICODENDRON*

1. Many branched trees or shrubs; the leaves arranged along the branches, distinctively petiolate.
   2. Leaves opposite; flowers yellow, sepals reflexed at anthesis, nectary a 4-dentate cup, adrogynophores centered, gynophores 3–5 cm, densely stellate; petals 5–7 mm wide; E Brazil ____ **C. yco**
   2. Leaves spirally, rarely subopposite on the same branch; flowers brown to greenish-brown, sepals erect at anthesis, nectary a 3-lobed cup, androgynophores off-centered, gynophores 5–8 cm, sparsely stellate; petals 10–15 mm wide; W Ecuador and adjacent northern Peru ____ **C. scabridum**
1. Unbrached to sparsely branched shrubs or treelets; the leaves whorled at the end of the terminal branches, sessile to 2 cm petiolate.
   3. Inflorescence a raceme with the flowers distinctively pedicellate, pedicels 1.8–4 cm, relatively laxly arranged on a short axis, 1–5 cm; gynophore 1.6–2 cm, ovary oblong; fruit oblong-ellipsoid; eastern Brazil ____ **C. bahianum**
   3. Inflorescence a racemose spike with the flowers subsessile, pedicels to 3 mm, densely arranged along the axis, 10–40 cm; gynophore 8–9 cm, ovary subglobose; fruits subglobose; NW Venezuela, near Valera ____ **C. valerabellum**

Rejected names

Colicodendron anceps Shuttl., *nomen* in Chapman, Fl. South. U.S. 32. 1860. = *Quadrella jamaicensis* (Jacq.) J. Presl.

Colicodendron angustifolium (Kunth) Hutch., Gen. Fl. Pl. 2:309. 1967. = *Quadrella angustifolia* (Kunth) H.H. Iltis & X. Cornejo.
Colicodendron avicenniafolium (Kunth) Seem., Bot. Voy. Herald 78. 1852. = *Beautempsia avicennifolia* (Kunth) Gaudich.
Colicodendron crotonoides (Kunth) Hutch., Gen. Fl. Pl. 2:309. 1967. = *Capparicordis crotonoides* (Kunth) H.H. Iltis & X. Cornejo.
Colicodendron lepidotum Turcz., Bull. Soc. Nat. Mosc. 27:327. 1854. = *Quadrella odoratissima* (Jacq.) Hutch.
Colicodendron longifolium Mart., Flora 22:26. 1839. = *Neocalyptrocalyx longifolium* (Mart.) X. Cornejo & H.H. Iltis.
Colicodendron obovatum Turcz., Bull. Soc. Nat. Mosc. 27:327. 1854. = *Monilicarpa tenuisiliqua* (Jacq.) X. Cornejo & H.H. Iltis.
Colicodendron pulchellum Seem., Bot. Voy. Herald 78. 1852, nomen = *Calanthea pulcherrima* (Jacq.) Miers.
Colicodendron salicifolium (Griseb.) Hutch., Gen. Fl. Pl. 2:309. 1967. = *Sarcotoxicum salicifolium* (Griseb), X. Cornejo & H.H. Iltis.
Colicodendron subbilobum (Kunth) Seem., Bot. Voy. Herald 78. 1852. = *Cynophalla flexuosa* (L.) J. Presl.
Colicodendron tweedianum (Eichl.) Hutch., Gen. Fl. Pl. 2:309. 1967. = *Capparicordis tweediana* (Eichl.) H.H. Iltis & X. Cornejo.

Uncertain name

Colicodendron obliquifolium Turcz., Bull. Soc. Nat. Mosc. 27:328. 1854.

We have not seen *Linden 1370*, the cited type specimen of *Colicodendron obliquifolium*, collected from "Nova Grenada, prov. Pamplona at ripas Rio Zulia" (Colombia). However, *Colicodendron obliquifolium*, originally described as "glabrum…," evidently does not belong to *Colicodendron*.

ACKNOWLEDGMENTS

Thanks are due to the following herbaria for sending their collections as loan or gift for this study: AAU, B, BKL, BM, CEPEC, CGE, CTES, DAV, F, GB, GH, GUAY, HEID, K, LD, LOJA, M, MO, NY, PEUFR, PR, QCA, QCNE, RSA, SEL, US, USF, USM, WIS. The first author had the pleasure to visit the herbaria: BKL, GUAY, LOJA, MO, QAP, QCA, QCNE, SEL and US. Ludwig Martins, Ulrike Starck and Hans-Joachim Esser provided valuable help with the types housed at B and M, respectively. R. Vogt (B) confirmed the Willdenow's handwritten on the label of the isolectotype of *Capparis scabrida* (B-W 10055-00 0). The second author gratefully acknowledges the financial aid of the University of Wisconsin-Madison Graduate School, the O.N. and E.K. Allen UW Herbarium Fund and the *Consejo de Desarrollo Científico y Humanístico de la Universidad Central de Venezuela* for financial help and sponsorship of the 1991 "Capparaceae Expedition" to Venezuela. Carmen Benítez de Rojas made valuable comments of *Colicodendron valerabellum*. The drawings and photo are mostly the talented artwork of Kandis Elliot, Marian Firmani (Fig. 3A–E), Bruno Manara (Fig. 4A, C), T. Ruiz Z. (Fig. 3F), and George Bunting (Fig. 6H, photo).

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BOOK REVIEW

Walter S. Judd, Christopher S. Campbell, Elizabeth A. Kellogg, Peter F. Stevens, and Michael J. Donoghue. 2007. **Plant Systematics: A Phylogenetic Approach (ed. 3).** (ISBN 978-0-87893-407-2, hbk.). Sinauer Associates, Inc., 23 Plumtree Road, Sunderland, Massachusetts 01375, U.S.A. (**Orders:** www.sinauer.com, fax 1-413-549-1118). $94.95, 620 pp., ca. 325 illustrations, 25 color plates, 8 1/2" × 11".

Chapters:

1. The Science of Plant Systematics
2. Methods and Principles of Biological Systematics
3. Classification and System in Flowering Plants: Historical Background
4. Taxonomic Evidence: Structural and Biochemical Characters
5. Molecular Systematics
6. The Evolution of Plant Diversity
7. An Overview of Green Plant Phylogeny
8. Lycophytes, Ferns and Their Allies, and Extant Gymnosperms
9. Phylogenetic Relationships of Angiosperms
Appendix I. Botanical Nomenclature
Appendix II. Specimen Preparation and Identification

For the third time, we look at plant classification with the authors and scientists Judd, Campbell, Kellogg, Stevens, and Donoghue. This is good news as it means that research on plant taxonomy and systematics as well as our understanding of the plant kingdom and the tools of science are all evolving.

I loved this textbook as it holds everything one needs to know about plants: families, floral formulas, distribution and ecology, genera and species, economic plants and products, references of articles and books, figures, phylogenetic trees and morphological character states, and a large discussion on DNA and problematic phylogenetic positions of groups. In addition, keys are provided along with pictures, tables of diagnostic features of some subfamilies, a nice glossary, and a DVD.

The above facts are the result of both intensive plant collecting and herbarium-based research (the practice of which is explained) and intensive thoughts on what a plant is, what systematics is, how the phylogenetic process works, and how we have historically handled the task of plant classification.

The book gives not only plant groups but also explains why a group is defined and delimited in a specific manner. The authors' approach is a phylogenetic one, which is the most current way of thinking in plant evolution as it considers together classical morphology and anatomy as well as DNA features.

Since the printing of the second edition of this textbook, some new concepts of grouping have evolved. For the non-flowering plants, (1) ferns are now called Moniliphytes instead of Moniliforms; (2) Marattiaceae, formerly within Ophioglossales, now constitutes its own order, Marattiales; (3) Polypodiales is now a subcategory of the "Leptosporangiate Ferns" instead of being the equivalent, meaning that some families of Polypodiales as defined in the second edition are now bumped up to Order-level taxa (e.g., Osmundaceae, formerly within Polypodiales, is now Osmundales). Regarding new classifications within the angiosperms, the "Magnoliid Complex" is identified as a clade in the third edition, meaning that Magnoliales, Laurales, Canellales, and Piperales form a monophyletic group.

I recommend this textbook for any classes that are botany-related, for any research projects that are botany-related, and any naturalist groups that are botany-related. Plants are wonderful: let people know more about them.—*Virginie H. Raquet, BRIT Research Associate, 13380 Plan-de-Cuques, France, vraquet@brit.org.*

REVISION OF *GONOLOBUS* S.S. (APOCYNACEAE: ASCLEPIADOIDEAE) IN THE WEST INDIES

Alexander Krings

Herbarium, Department of Plant Biology
North Carolina State University
Raleigh, North Carolina, U.S.A. 27695-7612

ABSTRACT

A revision of *Gonolobus* s.s. (Apocynaceae: Asclepiadoideae: Gonolobinae) in the West Indies is provided based on recent evidence of support for the monophyly of the genus from molecular and morphological data. Ten species are recognized (eight endemic to a single island each). Keys, descriptions, and illustrations are provided for all ten species. The conservation status of each species is provisionally assessed using IUCN and NatureServe criteria. *Gonolobus stapelioides* is neotypified. Two new combinations are made in *Matelea*: **M. dictyopetala** and **M. pubescens.**

RESUMEN

Se hace una revisión *Gonolobus* s.s. (Apocynaceae: Asclepiadoideae: Gonolobinae) en las Indias Occidentales basada en pruebas recientes que soportan la monofilia del género basada en datos moleculares y morfológicos. Se reconocen diez especies (ocho endémicas de una sola isla). Se aportan claves, descripciones, e ilustraciones de las diez especies. Se evalúa el estado de conservación provisional usando los criterios de IUCN y de NatureServe. Se neotipifica *Gonolobus stapelioides*. Se hacen dos combinaciones nuevas en *Matelea*: **M. dictyopetala** y **M. pubescens.**

INTRODUCTION

About fifty species of subtribe Gonolobinae (Apocynaceae: Asclepiadoideae) occur on the islands comprised by the Greater and Lesser Antilles, the Bahamas, Trinidad and Tobago, and Aruba and the Netherland Antilles. Evidence from the chloroplast (Rapini et al. 2003; Liede-Schumann et al. 2005; Rapini et al. 2006; Krings et al. 2008) and nuclear genomes (Krings et al. 2008) supports the monophyly of the subtribe. Genera referred to the subtribe with representation in the region include *Fischeria* DC., *Gonolobus* Michx., *Matelea* Aubl. (incl. *Ibatia* Decne., *Jacaima* Rendle, *Poicilla* Griseb., *Poicillopsis* Schltr., *Ptycanthera* Decne.), *Macroscepis* Kunth, and *Metalepis* Griseb. (Fontella & Schwarz 1981a; Kunze 1995; Liede 1997; Morillo 1997; Rapini et al. 2003; Liede-Schumann et al. 2005; Rapini et al. 2006). Subtribal position has been most controversial for *Metalepis*, which some workers have also placed within a broad *Cynanchum* L. (Woodson 1941; Spellman 1975; Sundell 1981). Recent evidence places it basal to a well-supported Metastelmatinae-Oxypetalinae-Gonolobinae clade (Liede & Kunze 2002; Liede-Schumann et al. 2005). The last regional treatment of Gonolobinae is now over 100 years old (Schlechter 1899) and a number of new species have recently been described by various workers, including Britton, Krings, Liogier, Proctor, Spellman, Urban, and Woodson (see Krings 2005b, 2006, 2007). Most members of the subtribe have never been monographed (Rapini et al. 2003) and the circumscription of most genera remains poorly defined. The *Gonolobus-Matelea* complex in particular is in desperate need of taxonomic revision. However, the size of the complex (ca. 200–350 spp.) requires an approach focusing on smaller, more tractable subgroups. Considering the support for a monophyletic *Gonolobus* s.s. based on recent evidence from chloroplast (*trnL-F*, *rps16*) and nuclear (*LEAFY*) data (Krings et al. 2008), recent taxonomic changes in West Indian taxa (Krings 2005a–d), and that several species have been published from the area since the last comprehensive treatment over a hundred years ago (Schlechter 1899; Krings 2006, 2007), a revision of the genus in the West Indies seemed appropriate. This revision treats all ten West Indian Gonolobinae species referable to *Gonolobus* s.s. (i.e., characterized by the presence of laminar, dorsal anther appendages, winged follicles, and a synapomorphic guanine; Krings et al. 2008). In addition, two new combinations are made in *Matelea*: *M. dictyopetala* and *M. pubescens* (see Doubtful and excluded names).

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METHODS

This treatment is based on critical study of ca. 250 specimens of the fifty some known species in West Indian Gonolobinae, obtained in part through: (1) loan requests from ninety herbaria—of which sixty-five responded with either loans, digital images, or negative search results (see Acknowledgements), (2) visits to BM, BSC, DUKE, HAC, HAJB, IJ, K, UCWI, UPRRP, US, and P, and (3) forty-eight days of field work by the author in the Bahamas (Long Island), Cuba, Dominica, Jamaica, Puerto Rico, St. Lucia, and St. Vincent. The treatment is also informed by analyses of sequences of portions of the chloroplast (*trnL-F*, *rps16*) and nuclear genomes (*LEAFY*) of selected accessions (see Krings et al. 2008). The species concept employed is an amalgam of the Phylogenetic Species Concept (PSC) of Nixon and Wheeler (1990) and the Evolutionary Species Concept (ESC) as modified by Wiley (1978), namely that: a species is a lineage of ancestral-descendent populations, which have maintained their identity from other such lineages, and which are diagnosable by a unique combination of character states in comparable individuals. Although the PSC has been critiqued as a non-historical concept—and thus potentially failing to identify instances of phenotypic homoplasy (Baum & Donoghue 1995)—this critique has not been accepted universally (Luckow 1995). The concept has been useful both as theoretical definition and operational delimitation criterion. However, as the application of the PSC, and its discovery method Population Aggregation Analysis (PAA; Davis & Nixon 1992), requires study of populations, its application is limited when entities are known uniquely from a population, or worse, from a single collection (e.g., *G. absalonensis*). In the absence of complete, multi-population accessions for extant and historical species, the provisional approach taken here is to rely on observable patterns of differentiation, with the general phytomonographic assumption that these patterns are due to a variety of biological processes underlying the morphological and historical integrity of species (McDade 1995). As a result, character states of each lone populational representative were assumed fixed and together used to form a population profile for PAA. Specimens representing each distinct aggregated population profile were considered to belong to distinct species, even if represented by only single collections, if they exhibited unique, qualitative morphological character states, unknown from other population profiles. As with any hypothesis, concepts of these species are open to modification and reinterpretation in light of any new collections.

The conservation status of treated species was provisionally evaluated by applying the criteria articulated in version 3.1 of the International Union for Conservation of Nature and Natural Resources (IUCN) Red List Categories and Criteria (IUCN 2001) and version 6.1 of the NatureServe Conservation Status Ranks (NatureServe 2006).

RESULTS

Ten species of *Gonolobus* are recognized from the West Indies, here defined to include the Bahamas, the Greater Antilles, and the Lesser Antilles (excl. Aruba, Bonaire, Curaçao, Trinidad, and Tobago; Fig. 1). All ten species are endemic to the region. Descriptions of the species are provided following a discussion of morphology and keys to the species. Corona morphological terminology follows Liede and Kunze (1993) and Kunze (1995): Ca = faucal annulus (corolline corolla); Cd = dorsal anther appendage; Ci = interstaminal gynostegial corona; C(is) = fused staminal and interstaminal gynostegial corona; Cs = staminal gynostegial corona. Species are arranged alphabetically. IUCN criteria justifying an assigned conservation category are listed following each category. Following Franz et al. (accepted), taxon concept mapping is provided to facilitate databasing. The operators <, =, and > are used to indicate whether a given taxon concept is respectively narrower than, equal to, or broader than a previously published concept. The symbol ≠ is used to indicate the misapplication of a name to a concept. Herbarium abbreviations follow Index Herbariorum (Holmgren & Holmgren 1998–present). Book abbreviations follow TL-2 (Stafleu & Cowan 1976–1988) and journal abbreviations B-P-H (Lawrence et al. 1968) and B-P-H/S (Bridson & Smith 1991). Author abbreviations follow Brummitt and Powell (1992).

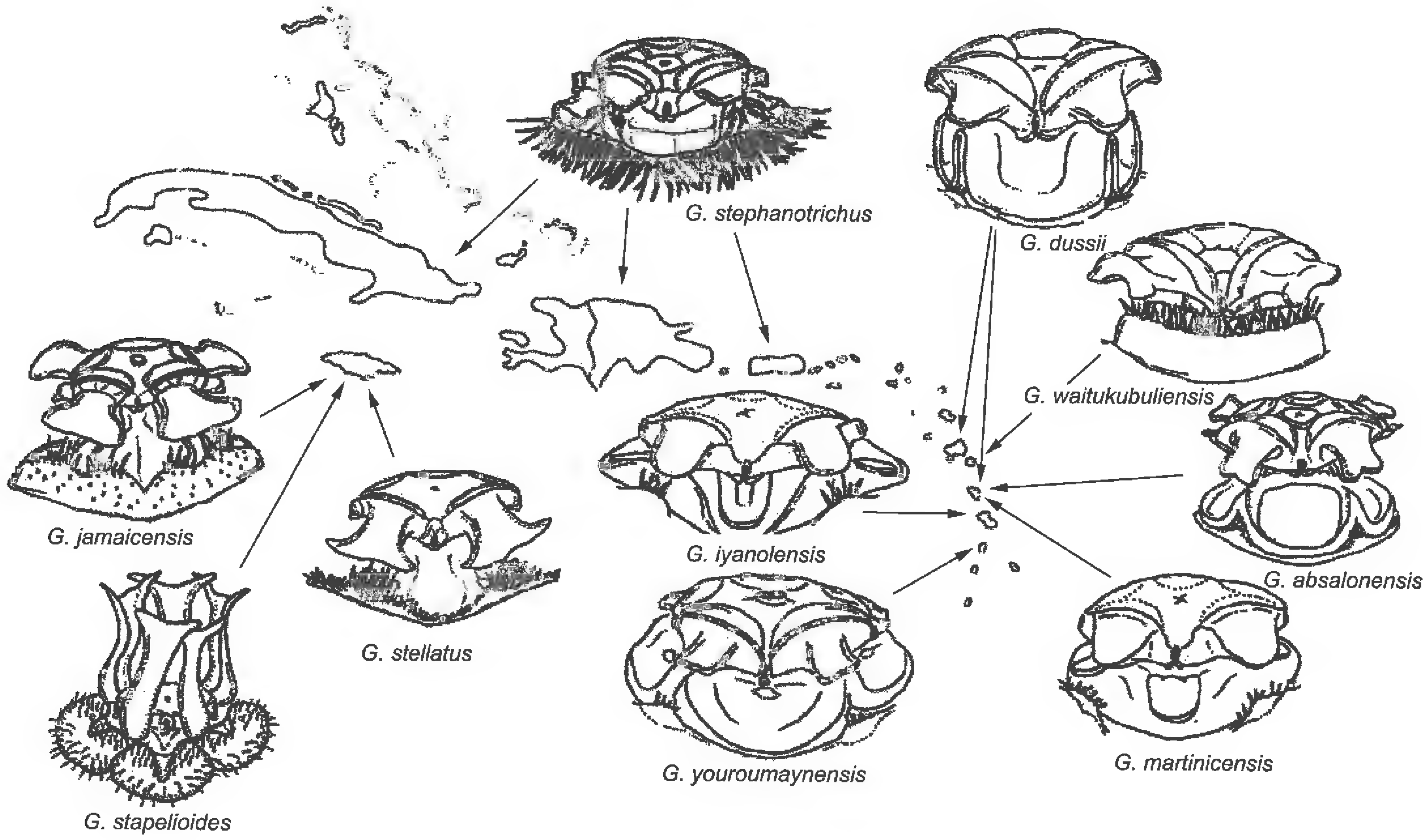

Fig. 1. Distribution of and gynostegial variation in *Gonolobus* in the West Indies.

TAXONOMIC HISTORY

The genus *Gonolobus* was erected by Michaux in 1803 based on a taxon from the southeastern United States—*Gonolobus suberosus* (L.) R.Br. Reveal and Barrie (1992) reviewed the complicated nomenclatural history of the type species and Krings and Xiang (2004, 2005) its taxonomy. About 318 names have been published in *Gonolobus*. Estimates of species numbers in the genus vary from 100 to 150 (Rosatti 1989; Mabberley 1997; Stevens 2001). The degree of variation is largely the result of still poorly known tropical taxa and differences regarding generic limits. Woodson (1941) considered that the genus *Gonolobus* should contain plants characterized by only long, eglandular trichomes, laminar dorsal anther appendages, and smooth, angled or winged follicles, whereas *Matelea* should contain plants characterized by glandular and eglandular trichomes, anthers lacking laminar dorsal appendages, and muricate follicles. Unconvinced that laminar dorsal anther appendages should serve as a generic character and citing examples of smooth [but not angled or winged] fruits in *Matelea*, Shinners (1950) argued against Woodson's generic concept and later included twelve of Woodson's (1941) *Gonolobus* combinations in *Matelea* (Shinners 1950, 1964). Drapalik (1969) essentially followed Shinners by maintaining the type of *Gonolobus* (i.e., *G. suberosus*, syn. *G. gonocarpos* (Walter) L.M. Perry) in *Matelea*, although noting its morphological distinctness vis-à-vis other subtribal members in the southeastern United States. Taking a broader geographical perspective of generic morphology, Rosatti (1989) argued for renewed circumscription of *Gonolobus* based on the presence of laminar dorsal anther appendages. Most recently the concept of *Gonolobus* as characterized by short, capitate-glandular, short acicular, and long acicular trichomes, laminar dorsal anther appendages (typically), and smooth, winged follicles has been used by Stevens (2001). However, glandular hairs, although thought characteristic of *Matelea* by Woodson (1941), also appear without circumscriptional value in the *Gonolobus-Matelea* question, being present in both the type of *Gonolobus* and numerous species lacking dorsal anther appendages (Rosatti 1989). Nonetheless, the monophyly of *Gonolobus*, whether narrowly or broadly circumscribed, was supported in a recent analysis of chloroplast and nuclear data (Krings et al. 2008). Although parsimony is equivocal on

whether laminar dorsal anther appendages evolved once in the most recent common ancestor of *Gonolobus* s.l., or once in *Gonolobus* s.s. and once in the *Fimbristemma* Turcz. group within *Gonolobus* s.l. (Fig. 2), the character remains restricted to the *Gonolobus* s.l. clade within Gonolobinae. Interestingly, winged follicles appear to have arisen twice independently and can be considered synapomorphic for both *Gonolobus* s.l. (Krings et al. 2008), as well as for a mostly West Indian ocellate-petaled complex that likely includes *Matelea acuminata* (Griseb.) Woodson, *M. bayatensis* (Urb.) Woodson, *M. correllii* Spellman, *M. costata* (Urb.) Morillo, *M. nipensis* (Urb.) Woodson, *M. oblongata* (Griseb.) Woodson, *M. pusilliflora* L.O. Williams, *M. rhamnifolia* (Griseb.) Krings, and *M. tigrina* (Griseb.) Woodson. None of these latter taxa exhibit laminar dorsal anther appendages. This putative complex did not evolve within the *Gonolobus* s.l. clade and may deserve independent generic recognition. Members of the complex tend to share morphological characters apparently rare in *Gonolobus* s.l., such as reticulate, ocellate corollas.

A monophyletic *Gonolobus* s.l. can be characterized by the presence of two synapomorphic indels in *LEAFY*, as well as winged follicles (Krings et al. 2008). A monophyletic *Gonolobus* s.s. can be characterized by a synapomorphic transversion in *trnL-F* (thymine to guanine) not shared by any of 154 other Asclepiadoideae species sampled across Secamoneae, Ceropegieae, Marsdenieae, and Asclepiadeae. The former circumscription (i.e., *Gonolobus* s.l.) essentially agrees with that of Woodson (1941), Rosatti (1989), and Stevens (2001), and stands in contrast to that of Shinners (1950) and Drapalik (1969). To remain monophyletic however, *Gonolobus* s.l. must include the *Matelea denticulata* (Vahl) Fontella & E.A. Schwarz complex. Considering the morphological and molecular distinctions between the three lineages in the *Gonolobus* s.l. clade (Fig. 2), recognition of three separate genera currently seems preferable to me.

MORPHOLOGY

A discussion of the morphology of species of *Gonolobus* s.s. (hereafter simply *Gonolobus*, unless otherwise specified) is provided below. The discussion concentrates on West Indian *Gonolobus* species, but when possible provides a broader context of variation within West Indian Gonolobinae.

Growth form.—Species of West Indian *Gonolobus* are twining vines, as are all currently known members of West Indian Gonolobinae (Fig. 3A). Older stems may become somewhat woody, but no collection or live plant has been seen by the author that approached 1 cm or greater in diameter. Individuals may climb as high as a few meters in gaps and openings.

Latex.—Latex is known for the following species: *Gonolobus iyanolensis* Krings, *G. jamaicensis* Rendle, *G. stapelioides* Desv. ex Ham., *G. stellatus* Griseb., *G. stephanotrichus* Griseb., *G. waitukubuliensis* Krings, and *G. youroumaynensis* Krings. It has been primarily described as either milky or white, observations confirmed by the author in the field for *G. iyanolensis*, *G. jamaicensis*, *G. stapelioides*, *G. stephanotrichus*, *G. waitukubuliensis*, and *G. youroumaynensis*. Latex was described by collectors as watery in a single instance—a Puerto Rican collection of a young sterile vine referred to *G. stephanotrichus* (*Acevedo-Rodríguez & Axelrod 7785*, US!). Published studies of latex chemistry in Gonolobinae are unknown to the author, although such inquiry would likely yield interesting results based on studies of other members of Asclepiadoideae (see Uses). Latex chemistry has been applied to solving taxonomic problems in Cynanchinae (Liede et al. 1993; Liede & Kunze 2002).

Pubescence.—Most members of subtribe Gonolobinae, exhibit at least two distinct trichome types, but frequently more. West Indian species of *Gonolobus* exhibit four types: (1) multi-cellular, sharp, eglandular, (2) uni-cellular, sharp, eglandular, (3) uni-cellular, glandular-capitate, and (4) papillate (Fig. 3B). Papillae appear to be restricted to the adaxial surface of the corolla lobes—typically borne only on the right side of the lobes. The remaining trichome types may be found anywhere else on the stem, leaves, inflorescences, or flowers, usually in combination. Multi-cellular, sharp, eglandular trichomes found on stems are primarily retrorse to retrorse-spreading internodally, but may be appressed-ascending along a narrow ridge connecting opposite petioles. In contrast to some other members of West Indian Gonolobinae (e.g., *M. corynephora* Krings, *M. linearipetala* Alain, *M. phainops* Krings, *M. rhynchocephala* Krings, *M. torulosa* Krings), stem trichomes in West Indian *Gonolobus* are not borne in two distinct lines.

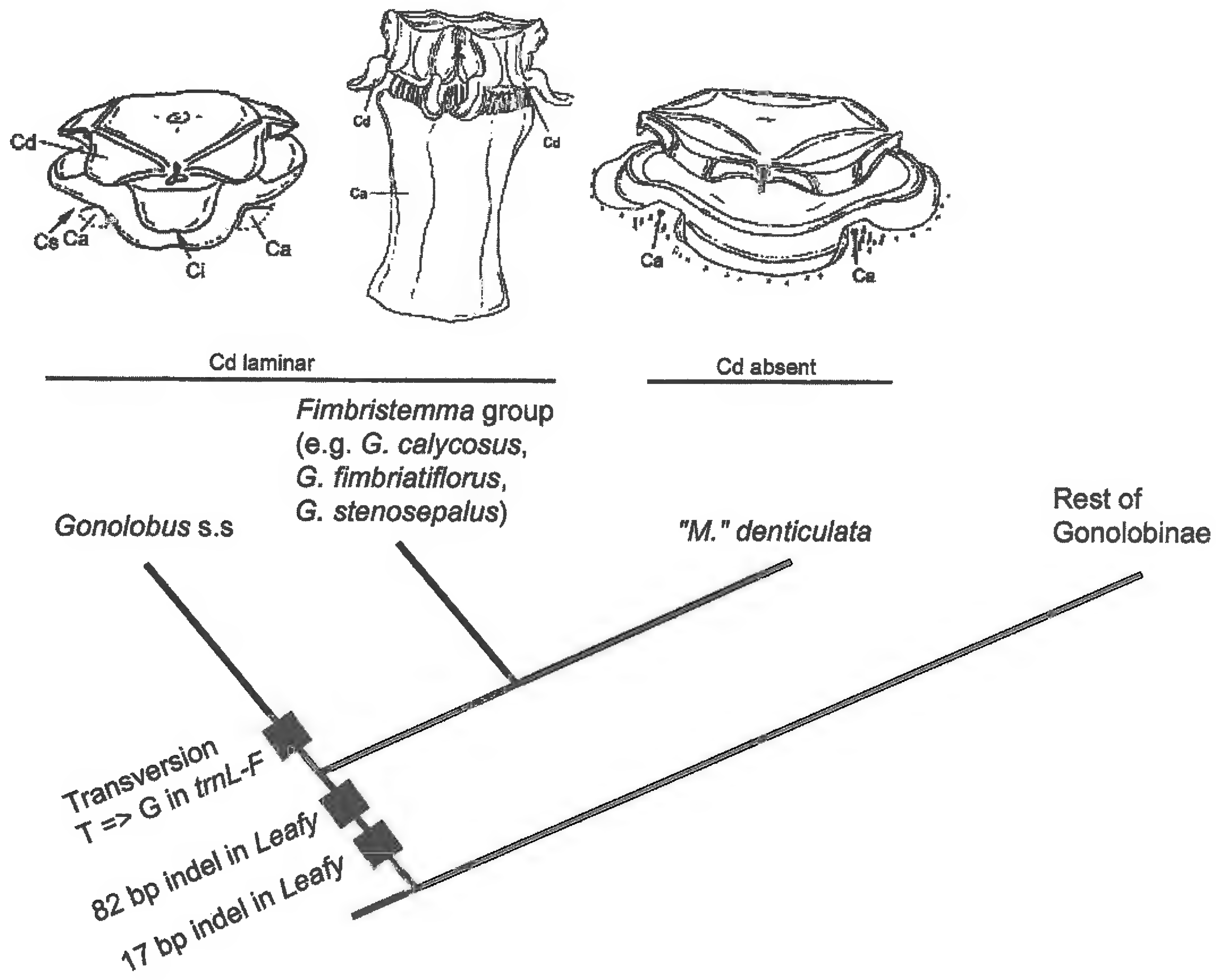

Fig. 2. Model of evolution of *Gonolobus* s.l. based on current evidence, with molecular synapomorphies mapped on branches (from Krings et al. 2008). Representative gynostegia shown are from left to right: *G. suberosus* (*Walker s.n.*, NCSC), *G. calycosus* (*Williams et al. 24759*, LL), and *M. denticulata* (*Dodson & Dodson 15450*, NY). Ca = faucal annulus of corolla; Ci = interstaminal gynostegial corona segment; Cd = laminar dorsal anther appendage; Cs = staminal gynostegial corona segment; *G.* = *Gonolobus*; *M.* = *Matelea*.

Leaves.—In general, species of *Gonolobus* exhibit simple, opposite, membranous, cordate leaves, although a few taxa, such as the Jamaican *G. stellatus*, *G. jamaicensis*, and *G. stapelioides*, exhibit truncate to cuneate leaf bases (Fig. 3A & C). The leaves of *G. jamaicensis* and *G. stapelioides* tend to be coriaceous. Leaf apices vary from acute to acuminate. Leaf size and shape may be influenced by position on the stem (e.g., basal vs. terminal) and habitat (e.g., edge vs. forest interior; sun vs. shade) (Krings, pers. obs.).

Laminar colleters.—In West Indian *Gonolobus* species, as in all West Indian Gonolobinae, two or more colleters are borne on the adaxial midrib near the junction of the leaf base and the petiole apex (Fig. 3D). Colleters vary from deltoid to lanceoloid.

Stipular colleters.—In West Indian *Gonolobus* species, a single colleter is borne on each side of the petiole at its extreme base (Fig. 3E). Colleters vary from deltoid to lanceoloid. Inter-petiolar (borne along a ridge or line between two opposing petioles at a node) colleters are rare and infra-petiolar (borne within the width of a petiole at its base) are apparently absent. Stipular colleters in other West Indian Gonolobinae vary in position, but frequently appear to be associated with the stem rather than the petiole.

Inflorescences.—Inflorescences of most West Indian Gonolobinae species, including all *Gonolobus* species in the area, are extra-axillary and racemose (umbelliform inflorescences appear to be restricted to Haitian *Matelea crispiflora* (Urb.) Jiménez). Inflorescences can be borne at nodes with immature leaves

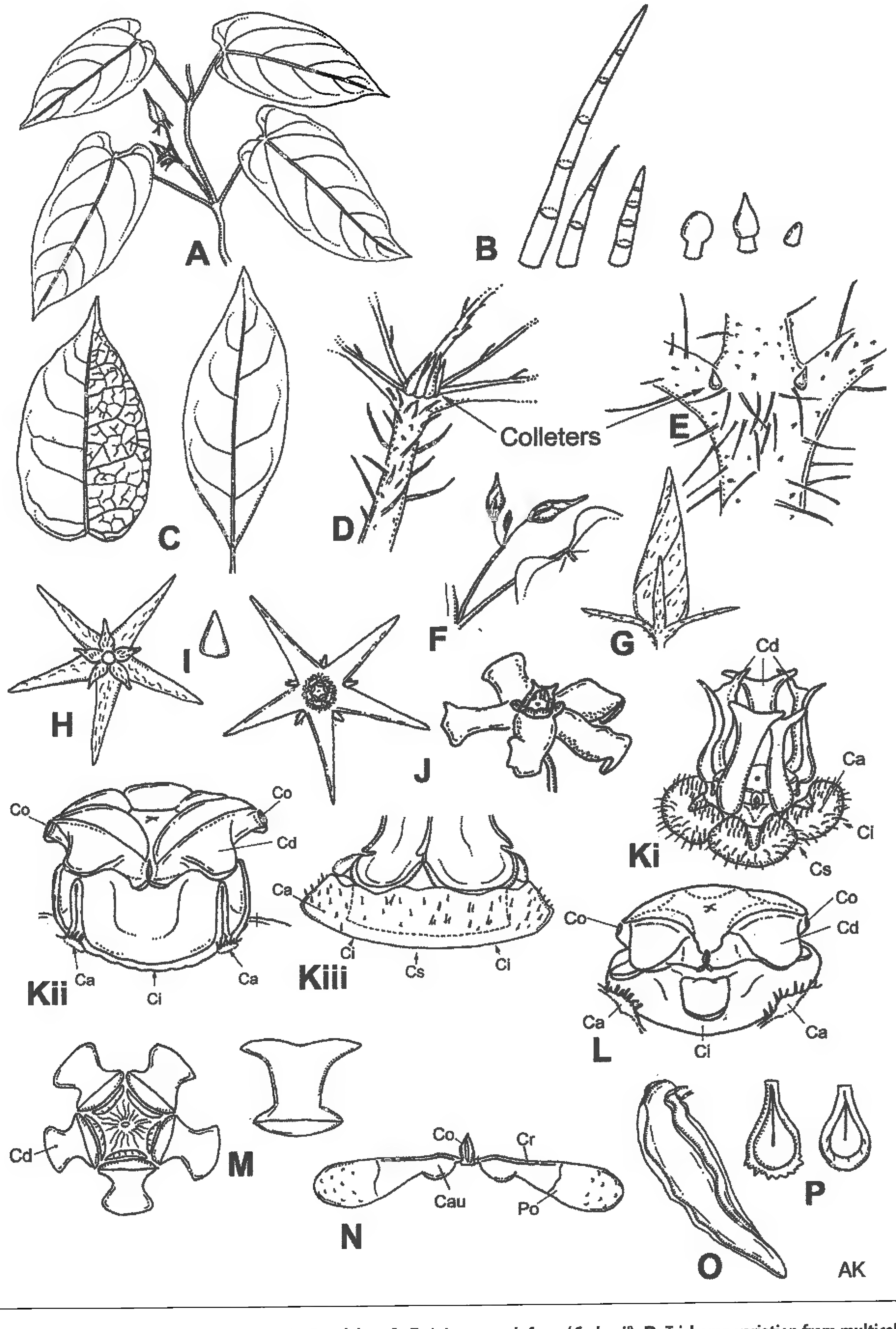

FIG. 3. Morphological characteristics and variation in *Gonolobus*. **A.** Twining growth form (*G. dussii*). **B.** Trichome variation from multicellular, sharp, eglandular (left three) to glandular capitate to papillate (rightmost) (*G. yourouymaynensis*, except papillae from corolla of *G. rostratus*). **C.** Variation in leaf shape (cordate: *G. jamaicensis*; cuneate: *G. stellatus*). **D.** Laminar colleters (*G. youroumaynensis*). **E.** Stipular colleters (*G. youroumaynensis*). **F.** Inflorescence (*G. tobagensis*). **G.** Dextrorse flower bud (*G. tobagensis*). **H.** Five-parted calyx (*G. stephanotrichus*). **I.** Calycine colleter (*G. stephanotrichus*). **J.** Variation in corollas (left: *G. stephanotrichus*; right: *G. stapelioides*). Ki–iii. Variation in faucal annuli, as well as gynostegial coronas (i: *G. stapelioides*; ii: *G. dussii*; iii: *G. jamaicensis*). **L.** Ligulate staminal segment of gynostegial corona (*G. martinicensis*). **M.** Variation in laminar dorsal anther appendages (left: *G. rostratus*; right: *G. stellatus*; see also Ki–ii, L). **N.** Pollinarium (*G. stephanotrichus*). **O.** Winged follicle (*G. stephanotrichus*). **P.** Seeds distally dentate (*G. iyanolensis*) and entire (*G. stephanotrichus*). **Ca** = faucal annulus of corolla; **Cau** = caudicle; Ci = interstaminal gynostegial corona segment; **Cd** = laminar dorsal anther appendage; **Co** = corpusculum; **Cr** = crest; **Cs** = staminal gynostegial corona segment; **Po** = pollinium.

as short as 1–3 cm long. The inflorescence is indeterminate and a series of flowers are produced on lateral pedicels from a single axis, the oldest at the base and the youngest at the apex (Fig. 3F). The axis is frequently significantly contracted and may not measure more than 1 cm in some species. In West Indian *Gonolobus*, bracts are frequently borne at pedicel bases, although they tend to be small and caducous in most species. For additional a review of inflorescence structure in other members of Asclepiadoideae, see Liede and Weberling (1995).

Based on specimens of West Indian *Gonolobus* seen in the course of the present study, one to three flowers may be open at a time. No phenological studies in West Indian *Gonolobus* have been undertaken and the life span of individual flowers remains unknown. Based on prior studies in Gonolobinae (see Lipow & Wyatt 1998; Krings 1999) and informal observation, it is unlikely that individual flowers last much longer than a week. In *Gonolobus suberosus* of the southeastern United States, individual flowers were open (2–) 4.61 (–10) days (N = 175; s.d. = 1.53) and inflorescences had open flowers for (2–) 8.96 (-23) days (N = 57; s.d. = 4.63) (Lipow & Wyatt 1998).

Aestivation.—The flowers of West Indian *Gonolobus* species are imbricate and dextrorse in bud (Fig. 3G). Imbricate aestivation is seen also in other members of West Indian Gonolobinae, but not all other genera exhibit dextrorse buds.

Calyces.—Calyces of *Gonolobus* species consist of five, green sepals (Fig. 3H). Apices are generally narrowly obtuse to rounded. Adaxial surfaces are uniformly glabrous. Abaxially surfaces vary from pubescent to glabrous. Frequently, the distal pedicel pubescence (when present) creeps onto the calyx base.

Calycine colleters.—West Indian *Gonolobus* species, as most members of West Indian Gonolobinae, bear 1–2 colleters in each sepal sinus (Fig. 3I). The colleters are deltoid to lanceoloid.

Corollas.—Corollas of West Indian Gonolobinae, including all *Gonolobus* species in the area, are 5-lobed (Fig. 3J). Corollas are generally subcampanulate to campanulate at the base with lobes spreading to reflexed. The corolla lobes of most species are planar. An exception is Jamaican *G. stapelioides*, which exhibits wavy and recurved corolla lobes. Corolla lobes of *Gonolobus* in the area slightly overlap at the base and frequently bear a minute glandular emergence in the sinus. Adaxial corolla coloration of West Indian *Gonolobus* species varies from uniformly green (most taxa) to burgundy tinged (*G. stephanotrichus*) to maroon (*G. jamaicensis*). Pubescence of the adaxial surfaces, when present, is limited to the faucal annulus and surrounding corolla lobe bases, and the right side of the corolla lobes.

Coralline coronas: Faucal annuli.—Faucal annuli—Ca sensu Liede and Kunze (1993), non sensu Woodson and Moore 1938 (see Kunze 1990, 1995)—are secondary annular thickenings of the tubular portion of the corolla (Fig. 3Ki–iii, L). Endress and Bruyns (2000) considered the Ca and Cc (coralline corona) of Liede and Kunze (1993) homologous, although Fishbein (2001) and Kunze (2005) explicitly rejected this hypothesis. Kunze (2005) noted that early ontogenetic stages of even taxa such as *G. lasiostemma* (Hemsl.) Woodson, which exhibits a Ca of five large fleshy lobes interstaminally (similar to Jamaican *G. stapelioides*), show a closed annular meristem at the initial stage. Faucal annuli (Ca) are distinctive in West Indian *Gonolobus* species and generally much more developed in members of this genus than in other West Indian Gonolobinae. Kunze (1995) found faucal annuli present in continental *Gonolobus* spp., as well as *Matelea lanata* (Zucc.) Woodson, and *Matelea dictyantha* Woodson, and absent in *Matelea argentinensis* (T. Mey.) Pontiroli and *Fischeria* spp. (all Gonolobinae). He also noted that outside Gonolobinae, faucal annuli were found mainly in some Stapelieae. The faucal annulus occurs immediately to the outside of the gynostegial corona (i.e., closer to the corolla lobes than the center of the flower). Annuli may be "interrupted" and reduced to a ridge opposite each corolla lobe sinus (e.g., *G. martinicensis* Decne.; Fig. 3L) or "uninterrupted" and well-developed (e.g., *G. jamaicensis*; Fig. 3Kiii). They are frequently pubescent, but not always, in contrast to the always glabrous, adjacent gynostegial coronas.

Gynostegial coronas.—Gynostegial coronas are quite varied in West Indian Gonolobinae (Fig. 3Ki–iii, L), but can be described conveniently in terms of staminal (Cs) and interstaminal (Ci) segments. The coronas have been interpreted as a "fusion" between the Cs and Ci (Liede & Kunze 1993), although it remains un-

clear whether the combined structure in fact represents a true fusion of disparate elements (see Endress & Bruyns 2000). In *Gonolobus*, the Cs region typically is raised and ridge-like, often meeting the lower portion of the laminar dorsal anther appendages (Cd). There are no instances of free, ligulate Cs segments as seen in other West Indian Gonolobinae taxa, such as *M. ovatifolia* (Griseb.) Woodson or *M. pentactina* Krings, or three-dimensionally complex Cs segments as seen in *M. tamnifolia* (Griseb.) Woodson and *M. oblongata*. Ci segments are single and cup-like in most West Indian *Gonolobus* species, and double (i.e., ligulate) only in *G. iyanolensis* and *G. martinicensis* (Fig. 3L). The interstaminal ligules of the double coronas of the latter two species are not positionally homologous with the staminal ligules seen in numerous species of *Matelea*, such as West Indian *M. ovatifolia* and *M. pentactina*, or continental *M. pubiflora* (Decne.) Woodson. However, some *Matelea* species, such as *M. maritima* (Jacq.) Woodson, also exhibit interstaminal ligules. In the Asclepiadoideae in general and West Indian *Gonolobus* in particular, the Ci region appears to serve as a holding cup for nectar secreted from a primary nectary on the flanks of the filaments inside the guide rail and in the stigmatic champer (Christ & Schnepf 1985, 1988). Among West Indian *Gonolobus* species, defined secondary nectaries are evident—at least as far as can be determined from herbarium specimens—only in a few species (e.g., *G. dussii* Krings). Kunze (1995, 1999) also found defined secondary nectaries in continental *G. chloranthus* Schltdl. and *G. fraternus* Schltdl., as well as the gonolobinoid *Matelea reticulata* (Engelm. ex A. Gray) Woodson and *M. argentinensis*. Secondary nectaries are epithelial, consisting of enlarged epidermal cells enriched with cytoplasm (Kunze 1995). Epithelial nectaries on the filament flanks appear to be widespread in Asclepiadoideae (Christ & Schnepf 1985; Kunze 1991; Kunze 1995).

The gynostegial stipe is generally edentate, although *G. jamaicensis*, *G. stephanotrichus*, and *G. youroumaynensis* have distinct teeth or "notches". The stipal teeth or "notches" of all three species are distinct in shape and occur in different locations. Their homology is unclear.

Laminar dorsal anther appendages.—Laminar dorsal anther appendages (Cd sensu Kunze 1995; Fig. 3Ki–ii, L–M) are restricted to *Gonolobus* s.l. or s.s., although it remains unclear whether they evolved once in the most recent common ancestor of the former, or once in the ancestor of the latter and in the ancestor of the *Fimbristemma* group within *Gonolobus* s.l. (Krings et al. 2008). Parsimony is equivocal on the question (Krings et al. 2008). The only other genus exhibiting dorsal anther appendages within Gonolobinae (and Asclepiadoideae, fide Kunze 1995) is *Fischeria*, but the appendages are vesicular rather than laminar (Murphy 1986; Vethacke 1994; Kunze 1995). Laminar dorsal appendages vary in shape from truncate to rounded to strongly, divergently bi-lobed. They tend to be spreading, but are conspicuously (and spectacularly) erect in mature flowers of *G. stapelioides* (Fig. 3Ki).

Style-heads.—Style-heads vary conspicuously in West Indian Gonolobinae, but tend to be essentially planar (varying from somewhat convex to somewhat concave) in *Gonolobus* species in the area (Fig. 3Kii, L). West Indian *Gonolobus* species also lack terminal style-head appendages, in contrast to other West Indian Gonolobinae species such as *Matelea maritima*, *M. corynephora*, *M. rhynchocephala*, and *M. torulosa* (see Krings 2006).

Pollinaria.—Pollinaria in Asclepiadoideae consist of a secreted corpusculum and two connected pollinia (pollen sacs; Kunze 1994). The two pollen sacs are the result of a reduction in anther locules from four in the more primitive Secamonoideae to two in the more derived Asclepiadoideae (Kunze 1996; Rapini et al. 2003; Liede-Schumann et al. 2005; Rapini et al. 2006). The pollinia are borne essentially horizontally in West Indian *Gonolobus* species—as they are in most members of the Gonolobinae—and should be considered broad, rather than long (Kunze 1995; Endress & Bruyns 2000; Fig. 3N). Only a portion of each pollinium is fertile and hyaline, sterile portions are easily visible. The corpusculum in the Gonolobinae (based on studies of *Matelea reticulata* and *M. argentinensis*) consists of solid side walls and a thick, three-layered floor (Kunze 1994). Kunze (1994) suggested that the formation of the side-walls originates in two primarily separated strands of secretion which eventually merge into one compact wall. Caudicles are present (Fig. 3N), but Kunze (1994) noted it was difficult to determine whether they are extensions of the outer flanks or new additions. He suggested the latter, based on the lack of staining with either hematoxylin or safranin, although

noting that caudicle initiation in the two *Matelea* species occurs very early in ontogeny and directly from the corpusculum, rather than apart from it.

Follicles.—Follicles in West Indian *Gonolobus* species (as in most continental *Gonolobus* spp. fide Stevens 2001), when known, are 5-winged (Fig. 3O), although small murications may be seen between the wings of some taxa (e.g., *G. stellatus*). Some continental species of *Gonolobus* also exhibit 4-winged (*G. albomarginatus* (Pittier) Woodson) or apparently 3-winged (*G. incerianus* W.D. Stevens & Montiel) follicles (Stevens 2001). Winged follicles are also exhibited by other members of West Indian Gonolobinae, such as *M. linearipetala*, and the putative members of an ocellate complex *M. acuminata*, *M. bayatensis*, *M. correllii*, *M. nipensis*, *M. oblongata*, *M. rhamnifolia*, and *M. tigrina*.

Seeds.—Seeds of West Indian *Gonolobus* species, as of most West Indian Gonolobinae, are essentially planar and pyriform in outline (distinctly plano-convex in *Matelea maritima* and *M. rubra* (H. Karst.) Spellman & Morillo). Distal margins vary from entire to dentate or crenate (Fig. 3P). Comas are translucent.

HABITAT

In general, West Indian *Gonolobus* species occur in small gaps or openings in mid-elevation, moist or wet forests on limestone derived soils. They are absent from high-elevation dwarf forests, coastal thickets, mangroves, marshes, or dry forests. Occurrences are infrequent to rare and likely limited by available habitat. Small gaps in minimally disturbed forests appear vital to seedling germination as vines are rarely encountered elsewhere. Changes in gap dynamics or forest condition, thus could have profound impacts on the maintenance of *Gonolobus* populations. With the exception of *G. youroumaynensis*, the species have not been found along roadside edges, where other vines (particularly *Ipomoea* L. spp. and *Dioscorea* L. spp.) are generally superior competitors and quickly form thick, tangled thickets. *Gonolobus youroumaynensis* was found along a roadside patch of vegetation in St. Vincent, although it remains unclear whether the population is competitive there or merely persistent following a colonization event. A population of *Gonolobus iyanolensis* persists on top of Gros Piton in St. Lucia among boulders.

POLLINATION

As there have been no pollination biology studies on West Indian *Gonolobus* species, their pollinators remain unknown. In fact, pollinators appear to be documented for only two species of *Gonolobus* range wide: *G. fraternus* (Mexico and Central America) and *G. suberosus* (United States).

Kunze (1999) studied the pollination ecology of *G. chloranthus* and *G. fraternus*, but was able to observe putative pollinators only on the latter. Pollinarium uptake was confirmed for two diptera species (Calliphoridae, Tachinidae), a bee (Apidae), and a wasp (Vespidae) (Kunze 1999). Other observed visitors included *Apis mellifera* Linnaeus (Apidae) and unidentified butterflies (Lepidoptera) (Kunze 1999). However, pollinarium removal by these could not be verified. Corpuscula were removed by the wasp and bee by their legs, and by the bee and the flies by their probosces. Foraging behavior differed among the observed species, with the wasp and bee prefering upper regions of the studied vine, and the flies, the middle and lower.

Drapalik (1969) captured small dipterans (all Chloropidae) on flowers of *G. suberosus*, but it remains unclear whether they are effective pollinators due to their size (1.5–3 mm) and lack of pollinaria on capture. Lipow and Wyatt (1998) also studied *G. suberosus*, but despite daily and nightly searches were unable to find pollinators.

Gonolobus suberosus appears to exhibit considerable variation in the numbers of flowers per individual plant, the number of flowers per inflorescence, and the number of inflorescences per individual plant (Lipow & Wyatt 1998). Only a small fraction of plants monitored by Lipow and Wyatt (1998)—less than 5%—were pollinated and per flower removal rate of pollen was only 0.31. This rate was less than previous reports in other asclepiads (Table 1).

Ollerton and Liede (1997) noted that subtribe Gonolobinae appears distinct in being predominantly dipteran pollinated, although this claim was based on only five *Matelea* species in the southeastern United

Table 1. Per flower rates of pollen removal and pollinium deposition within Asclepiadoideae (arranged by per flower rate of pollen removal).

Species	Per flower rate of pollen removal	Per flower rate of pollinium deposition	Source
Asclepias exaltata L.	0.23–1.38	0.39–0.66	Queller (1985); Wyatt & Shannon (1986); Broyles & Wyatt (1990, 1995)
Gonolobus suberosus (L.) R.Br.	0.31	0.043	Lipow & Wyatt (1998)
Matelea reticulata (Engelm. ex A. Gray) Woodson	0.54–0.94	--	Liede (1994); Krings (1999)
Asclepias curassavica L.	0.62–1.7	0.13	Wyatt (1980); Willson & Melampy (1983); Wolfe (1987)
Asclepias syriaca L.	0.62–1.7	--	Willson & Rathcke (1974)
Asclepias quadrifolia Jacq.	0.81–2.41	--	Chaplin & Walker (1982)
Asclepias tuberosa L.	1.64	0.71	Wyatt (1978)
Funastrum pannosum (Decne.) Schltr.	2.43–2.48	0.57–1.52	Kunze & Liede (1991)
Funastrum clausum (Jacq.) Schltr.	2.64	2.16	Kunze & Liede (1991)
Asclepias solanoana Woodson	2.91–4.3	1.23–1.81	Lynch (1977)

States (Drapalik 1969). The claim remains mostly true today, although knowledge from only a single additional species of *Fischeria* and *Gonolobus* each has been added (Skutch 1988; Kunze 1999). Two additional studies examined species also studied by Drapalik (1969) and found additional dipteran floral visitors (Liede 1994; Krings 1999). Kunze (1999) found flowers of *G. fraternus* polyphilic and noted that they were not specialized for a single kind of pollinator. The ASCLEPOL database (http://www.uni-bayreuth.de/departments/planta2/research_wgl/ pollina/as_pol_d.html) currently also lists pollinators for *G. argentinensis* T. Mey. (1 sp. of Calliphoridae, Diptera), but this species has most recently been recognized in *Matelea*.

INSECTS HOSTED

There are no published records of insects hosted by West Indian *Gonolobus* species known to the author. However, a few records of primarily dipterans and lepidopterans have been published for continental species in the genus. Castrejon-Ayala and Camino-Lavin (1991) reported *Gonolobus sorodius*, nom. nud., as host for papaya fruit fly (*Toxotrypana curvicauda* Gerstaecker)—the principal insect pest of commercial papaya (*Carica papaya* L.). Norrbom (unpubl.) suggested this plant may be *Gonolobus barbatus* Kunth. Baker et al. (1944) reported another asclep host plant of papaya fruit fly—a wild species known as *talayote* or *talayotillo* in northeastern Mexico (Santa Engracia and Cañon de Rosario). Castrejón-Ayala (1987) suggested the plant may be a species of *Gonolobus* and Landolt (1994) suggested perhaps *G. erianthus* DC. *Gonolobus salvinii* Hemsl.—commonly called *champeron* in Guatemala—may yet be another host for the papaya fruit fly (Norrbom & Muñiz, unpubl.).

Capinera (2005) reported "*Gonolobus* sp." among hosts for the saltmarsh caterpillar (*Estigmene acrea* (Drury))—a species ranging from Canada to Central America. An unidentified species of *Gonolobus* was reported as host for *Erinnyis obscura obscura* (Fabricius)—a sphingid found in Amazonas, Brazil (Silva Motta & Xavier-Filho 2005).

There are a number of reports of *Gonolobus laevis* Michx. serving as host plant for various lepidopterans, including *Danaus gilippus* Cramer and *D. plexippus* (Linnaeus), however *G. laevis* belongs to the Cynanchinae, not Gonolobinae, and should be recognized as *Cynanchum laeve* (Michx.) Pers. (Liede & Täuber 2002).

SEED DISPERSAL

The follicles of known West Indian *Gonolobus* species are smooth and uniformly 5-winged, dehiscing along a solitary suture between two wings to release the comose seeds. Seeds are very light (Table 2) and can travel on slight breezes. Unfortunately, mature follicles have been documented by collections for only three

of the ten species of West Indian *Gonolobus* (Table 2). Immature follicles are known for *G. stapelioides* (see Additional specimens examined). The paucity of fruiting collections is echoed in West Indian Gonolobinae as a whole. Follicles have been collected for less than half of the estimated fifty species in the West Indies (Krings, unpubl.). The low rate of fruit collections may be due to naturally low levels of fruit set in the subtribe (Lipow & Wyatt 1998), as well as collector habit, flowers being necessary for most species level determinations. Lipow and Wyatt (1998) suggested that low fruit set in Gonolobinae may be attributable to pollen limitation. Less than 5 % of flowers monitored were pollinated and only a single fruit matured from 352 flowers on 13 plants (Lipow & Wyatt 1998).

CHROMOSOMES

There are no published reports of chromosome numbers in West Indian *Gonolobus* or Gonolobinae. Previously published reports for continental Gonolobinae, including continental *Gonolobus*, show the same basic chromosome number x = 11 that predominates the subfamilies Asclepiadoideae, Periplocoideae, and Secamonoideae (Albers & Meve 2001). Only 6% of 672 species surveyed in the three subfamilies by Albers and Meve (2001) were polyploid and deviations (reductions or increases in chromosome numbers) were found only in the Asclepiadoideae. No deviations within the Gonolobinae from 2n = 22 were found by Albers and Meve (2001), although only five species in four genera were included from the subtribe in their survey.

USES

As there are no published accounts of human uses of West Indian *Gonolobus* species known to the author, a survey of uses in other areas may be of interest to the reader. The Ecuadorian endemic and IUCN Vulnerable (VU) listed *Gonolobus saraguranus* Morillo has been reported to be used by the Saraguro native people as a medicinal plant (specific use unspecified), under the name *sacha ango* (Pitman 2003). Unspecified medicinal uses are also reported for *Gonolobus yucatanensis* (Woodson) W.D. Stevens, a taxon described in *Trichostelma* Baill. (Durán García et al. 1997). Standley and Williams (1969) noted that the tender, young fruits of *Gonolobus* species are commonly used as vegetables in Guatemala, and may be available in local markets under the name *cuchamper*, although this name has also been applied to the fruits of related genera. Specific uses are noted by Standley and Williams (1969) for *G. salvinii* (tender follicles eaten raw when almost mature, and cooked and eaten at almost all stages of growth) and *G. stenanthus* (Standley) Woodson (young follicles boiled or otherwise cooked with sugar to make sweetmeats or dulces). Stevens (2005) noted that "most, if not all, species of *Gonolobus* have fruits that are eaten when young, either raw or cooked." Numerous studies have examined potential medicinal properties of latex in Asclepiadinae (*Asclepias* L.: Liggieri et al. 2004; *Calotropis* R.Br.: Rasik et al. 1999; Kumar et al. 2001; Dubey & Jagganadham 2003; Shivkar & Kumar 2003; Ahmed et al. 2004; Alencar et al. 2004; Kumar & Shivkar 2004a & b; Shivkar & Kumar 2004; Al-Mezaine et al. 2005; Arya & Kumar 2004, 2005; Iqbal et al. 2005; Pahdy & Kumar 2005; Rajesh et al. 2005; Roy et al. 2005; Sehgal & Kumar 2005; Soares et al. 2005; Choedon et al. 2006; Kumar et al. 2006; Ramos et al. 2006a & b; Sehgal et al. 2006), Metastelmatinae (*Funastrum* E. Fourn.: Morcelle et al. 2004; *Philibertia* Kunth: Sequeiros et al. 2005), and Oxypetalinae (*Araujia* Brot.: Priolo et al. 2000; Gaig et al. 2005; *Morrenia* Lindl.: Vairo Cavalli et al. 2003), but no such studies are known to the author in Gonolobinae.

CONSERVATION

Human disturbance disproportionately affects infrequent plant species more than common taxa as further reductions of already low population sizes may not be sustainable (Lawton 1993; Casagrandi & Gatto 2000; Hendrix & Khyl 2000; Benítez-Malvido & Martínez-Ramos 2003). West Indian *Gonolobus* species, as many other species of Asclepiadoideae (Kunze & Liede 1991), appear to be quite infrequent, if not rare, and are in need of serious survey (particularly in Cuba and the Lesser Antilles) to establish their conservation status. However, some provisional remarks are possible, based on study of collections and field observations associated with this study.

TABLE 2. Seed weight and size in West Indian *Gonolobus* species for which mature fruits have been seen by the author. Arranged from lightest to heaviest seed. Seeds obtained from a single follicle for each species.

Species	Average seed weight [N = number of seeds sampled]	Length[1]	Width1
G. stephanotrichus (*Acevedo-Rodríguez 11445*, UPRRP)	0.0035 g [N=10]	(7.1) 7.4 (7.8) [N=10; s.d.=0.2066]	(3.4) 4.23 (4.7) [N=10; s.d.=0.4083]
G. stapelioides (*Bellingham 1487*, BM)	0.0044 g [N=81]	(4.6) 5.0 (5.6) [N=10; s.d.=0.2914]	(2.5) 2.93 (3.5) [N=10; s.d.=0.2627]
G. iyanolensis (*Graveson s.n.*, NCSC)	0.0116 g [N=26]	(8.8) 9.92 (10.5) [N=10; s.d.=0.4848]	(4.9) 5.38 (5.9) [N=10; s.d.=0.3084]

[1]Format for length and width measurements = (Min) Avg (Max) [number of seeds sampled; standard deviation]

The habitat requirements of West Indian *Gonolobus* species are in need of further study, but preliminary evidence suggests that most species are largely limited to small gaps or openings in mid-elevation, moist or wet forests. They appear to be poor competitors along forest edges. The combined infrequency of occurrence of individuals, poor competitive ability along edges, likely low pollination and fruit set rates (see Pollination and Seed Dispersal above), and need for small gaps or openings in specific forest community types, suggests that *Gonolobus* species may be particularly vulnerable to loss of habitat. This is of particular concern considering the high rate of island endemism among the species. Eight of the ten West Indian *Gonolobus* species are endemic to single islands (Fig. 1). *Gonolobus dussii* occurs on two islands and *G. stephanotrichus* occurs on three islands. Seven of the ten West Indian *Gonolobus* species are known from five or fewer collections or localities (Table 3). None of the remaining three species appears to be known from more than ten localities. Provisional estimates of conservation status according to the criteria outlined in Version 3.1 of the IUCN Red List Categories and Criteria (IUCN 2001) and Version 6.1 of NatureServe Conservation Status Ranks (NatureServe 2006) are provided in Table 3. Provisional estimates are based on historical collections, the number of known localities, whether taxa are known from protected areas, and inferred habitat or population changes. These estimates need to be followed by targeted survey to better establish the conservation status of the species.

TAXONOMIC TREATMENT

Gonolobus Michx., Fl. Bor.-Amer. 1:119. 1803. TYPE: *G. macrophyllus* Michx., nom. illeg. (*Vincetoxicum gonocarpos* Walter; *Gonolobus gonocarpos* (Walter) Perry (LECTOTYPE, designated by Perry 1938) = *Gonolobus suberosus* (L.) R.Br.

Rhizomatous, perennial vines. Leaves opposite, blades simple, membranous or coriaceous, apices obtuse, acute, or acuminate, bases mostly cordate, but cuneate to rounded in some taxa; colleters present on the adaxial surface at the base of the midvein. Stipular colleters 2, one borne at the base of the petiole on each side. Inflorescences extra-axillary, racemiform. Floral aestivation imbricate, dextrorse. Sepals 5; colleters 1–2 per sinus. Corolla lobes 5, mostly uniformly colored with various shades or green to reddish or maroon, sometimes multi-colored and basally maroon or dark purplish and apically green (e.g., *G. suberosus*), not ocellate, lobes overlapping at the base, glandular emergences present in the sinuses. Faucal annulus (Ca) present, sometimes interrupted and developed only in the staminal—or rarely interstaminal (e.g., *G. stapelioides*)—position. Gynostegial corona of fused staminal (Cs) and interstaminal parts (Ci); Cs not foliolate or free, not ligulate; Ci ligulate or not. Laminar dorsal anther appendages (Cd) present, reflexed, spreading, or erect. Style-head flat to slightly concave or convex, lacking a defined protuberance or elongate terminal appendage. Pollinaria with pollinia borne horizontally or essentially so. Follicles winged. Seeds essentially plane, distally entire or dentate, comose. 100–150 species (10 spp. in the West Indies as here defined).

Perry (1938) chose *Gonolobus macrophyllus* Michx.—the first of three species listed by Michaux (loc. cit.)—as the lectotype for the genus *Gonolobus*. However, Michaux cited *Vincetoxicum gonocarpos* Walter as a

TABLE 3. Number of collections and localities, distribution, and provisional conservation status of West Indian *Gonolobus* species. Arranged by number of localities represented, then number of collections. NatureServe conservation ranks follow IUCN ranks. IUCN conservation ranks are global. Critically endangered taxa are unknown from protected areas.

Species	No. of localities	No. of collections	Distribution	Provisional conservation status
G. absalonensis	1	1	Martinique	Critically endangered (CR); GH NH
G. martinicensis	1–3	3	Martinique	Critically endangered (CR); GH NH
G. youroumaynensis	1–2	3	St. Vincent	Critically endangered (CR); G1 N1
G. dussii	5	5	Guadeloupe and Martinique	Critically endangered (CR); GH NH (both islands)
G. iyanolensis	2	5	St. Lucia	Endangered (EN); G1 N1
G. stellatus	4	4	Jamaica	Vulnerable (VU); G3 N3
G. jamaicensis	4	5	Jamaica	Vulnerable (VU); G3 N3
G. waitukubuliensis	4–8	17	Dominica	Vulnerable (VU); G3 N3
G. stapelioides	5–7	13	Jamaica	Least concern (LC); G4 N4
G. stephanotrichus	7–10	19	Greater Antilles	Least concern (LC); G4 N4 (all islands of occurrence)

GH: Possibly Extinct (species)—Missing; known from only historical occurrences but still some hope of rediscovery. G1: Critically Imperiled—At very high risk of extinction due to extreme rarity (often 5 or fewer populations), very steep declines, or other factors. G3: Vulnerable—At moderate risk of extinction due to a restricted range, relatively few populations (often 80 or fewer), recent and widespread declines, or other factors. G4: Apparently Secure—Uncommon but not rare; some cause for long-term concern due to declines or other factors. NH: Possibly Extirpated (Historical)—Species or community occurred historically in the nation or state/province, and there is some possibility that it may be rediscovered. Its presence may not have been verified in the past 20-40 years. N1: Critically Imperiled—Critically imperiled in the nation or state/province because of extreme rarity (often 5 or fewer occurrences) or because of some factor(s) such as very steep declines making it especially vulnerable to extirpation from the state/province. N3: Vulnerable—Vulnerable in the nation or state/province due to a restricted range, relatively few populations (often 80 or fewer), recent and widespread declines, or other factors making it vulnerable to extirpation. N4: Apparently Secure—Uncommon but not rare; some cause for long-term concern due to declines or other factors.

synonym for his *G. macrophyllus*, rendering the latter name illegitimate. Perry (1938) proposed the combination *G. gonocarpos* as the correct name for Michaux's *G. macrophyllus*. Recent study found the entity variously known as *G. gonocarpos* or *G. macrophyllus* conspecific with *G. suberosus* (Krings & Xiang 2004, 2005). The latter name has priority following Reveal and Barrie (1992).

Some Robert Brown names have sometimes been incorrectly dated. In 1810, a preprint of his "On the Asclepiadeae, a Natural Order of Plants separated from the Apocinae of Jussieu" was made available. This same work later appeared in the first volume of the 1811 Memoirs of the Wernerian Natural History Society (Stearn 1960; Stafleu & Cowan 1976; Mabberley 1985). Although sometimes incorrectly cited from the first reading of the paper in 1809, communication at public meetings does not constitute effective publication (Forster 1991; Greuter et al. 2000; McNeill et al. 2006). Names should also not be ascribed to the 1811 appearance of the Memoirs of the Wernerian Natural History Society but rather to the preprint released in 1810. Thus the combination *Gonolobus suberosus* (L.) R. Br. should be cited as above, rather than in Mem. Wern. Nat. Hist. Soc. 1:35 (1810). As Brown's 1810 combination in Asclepiadeae is validly published (by definite association of the final epithet with the genus name), it takes priority over the Schultes combination in Systema Vegetabilium 6:59 (1820).

KEY TO THE SPECIES OF *GONOLOBUS* IN THE WEST INDIES

1. Corolla lobes with lateral margins revolute; faucal annulus (corolline corona or Ca) interrupted, strongly developed into two mounds opposite each corolla lobe, appearing absent opposite each corolla sinus, pubescent; laminar dorsal anther appendages erect (spreading when immature or spent), white, to 4.2 mm long, apices divergently and sharply bilobed ________ **6. G. stapelioides**

1. Corolla lobes essentially plane, sometime reflexed, but margins not revolute; faucal annulus (coralline corona or Ca) uninterrupted or if interrupted then at most developed into a shallow ridge opposite each corolla lobe sinus; laminar dorsal anther appendages (Cd) descending or spreading, variously colored, < 2 mm long, apices rounded, truncate, slightly emarginate, or rounded-bilobed (divergently and sharply bilobed only in *G. stellatus*).
  2. Faucal annulus of corolla (coralline corona or Ca) an uninterrupted ring, conspicuously raised (0.4–0.9 mm tall), pubescent along the entire rim or only opposite each corolla lobe sinus; gynostegial corona basally fused into an erect ring, obscured from view by the faucal annulus.
    3. Gynostegial stipe edentate _____ **9. G. waitukubuliensis**
    3. Gynostegial stipe dentate.
      4. Adaxial corolla lobes purple-red to marroon; gynostegial stipe teeth appearing as notches, borne on the lower portion of the column, just above the upwardly rising segment of each Cs; Jamaica _____ **4. G. jamaicensis**
      4. Adaxial corolla lobes various shades of green; gynostegial stipe teeth not appearing as notches, instead truncate, borne on the lower portion of the column, just above the upwardly rising segment of each Cs; Cuba, Hispaniola, Puerto Rico _____ **8. G. stephanotrichus**
  2. Faucal annulus of corolla (coralline corona or Ca) reduced to an interrupted ridge, distinct only opposite each corolla lobe sinus, tufted pubescent to glabrate or, if uninterrupted, then very shallow, to 0.25 mm tall; gynostegial corona not basally fused into an erect ring that is obscured from view by the faucal annulus.
  5. Interstaminal gynostegial corona double (i.e., a narrower upper ligulate corona lobe occurring on top of the broader lower corona).
    6. Corolla robust, base of corolla tube subcampanulate, as broad as long or broader than long; horizontal length of lower interstaminal gynostegial corona (Ci) from base of stipe to lobe apex 1.1–1.4 mm, narrow upper ligulate corona lobe of the Ci abruptly ending in a scooped out depression before reaching the stipe base, dorsally ridged _____ **3. G. iyanolensis**
    6. Corolla slender, base of corolla tube elongate-campanulate, distinctly longer than broad; horizontal length of interstaminal gynostegial corona (Ci) from base of stipe to lobe apex ≤ 0.7 mm, narrow upper ligulate corona lobe of the Ci ending essentially at the stipe base, dorsally plane or sometimes slightly raised into a shallow bump _____ **5. G. martinicensis**
  5. Interstaminal gynostegial corona single.
    7. Gynostegial stipe with a single tooth below each anther.
      8. Faucal annulus pubescent along the entire ring; teeth of gynostegial stipe borne on lower portion of the column, just above the upwardly rising segment of the Cs _____ **8. G. stephanotrichus**
      8. Faucal annulus pubescent only in the staminal position; teeth of gynostegial stipe borne on upper portion of the column, just below the anther _____ **10. G. youroumaynensis**
    7. Gynostegial stipe edentate.
      9. Cs to 1 mm tall; interstaminal gynostegial corona (Ci) with two distinctly raised and rounded mounds; laminar dorsal anther appendages (Cd) truncate or rounded _____ **2. G. dussii**
      9. Cs < 0.3 mm tall; interstaminal gynostegial corona (Ci) smooth, lacking raised bumps; laminar dorsal anther appendages (Cd) emarginate.
        10. Leaf bases uniformly cuneate; laminar dorsal anther appendages (Cd) slightly emarginate to divergently and sharply bilobed _____ **7. G. stellatus**
        10. Leaf bases cordate; laminar dorsal anther appendages rounded bilobed _____ **1. G. absalonensis**

REGIONAL KEYS TO THE SPECIES OF *GONOLOBUS*

GREATER ANTILLES

1. Corolla lobes with margins revolute; faucal annulus (coralline corona or Ca) interrupted, strongly developed into two mounds opposite each corolla lobe, absent opposite each corolla sinus, pubescent; laminar dorsal anther appendages erect (spreading when immature or spent), white, apices divergently and sharply bilobed, to 4.2 mm long; Jamaica _____ **6. G. stapelioides**
1. Corolla lobes essentially plane, sometime reflexed, but not revolute; faucal annulus (coralline corona or Ca) uninterrupted or if interrupted then at most developed into a shallow ridge opposite each corolla lobe sinus; laminar dorsal anther appendages (Cd) descending or spreading, variously colored, apices rounded, truncate, slightly emarginate, or rounded-bilobed (divergently and sharply bilobed only in *G. stellatus*), < 2 mm long.
  2. Faucal annulus of corolla (coralline corona or Ca) an uninterrupted ring, conspicuously raised (0.4–0.9 mm tall), pubescent along the entire rim or only opposite each corolla lobe sinus; gynostegial corona basally fused into an erect ring, obscured from view by the faucal annulus.

3. Adaxial corolla lobes purple-red to marroon; gynostegial stipe teeth appearing as notches, borne on the lower portion of the column, just above the upwardly rising segment of each Cs; Jamaica ________ **4. G. jamaicensis**
3. Adaxial corolla lobes various shades of green; gynostegial stipe teeth not appearing as notches, instead truncate, borne on the lower portion of the column, just above the upwardly rising segment of each Cs; Cuba, Hispaniola, Puerto Rico ________ **8. G. stephanotrichus**
2. Faucal annulus of corolla (corolline corona or Ca) reduced to an interrupted ridge, distinct only opposite each corolla lobe sinus, tufted pubescent to glabrate or, if uninterrupted, then very shallow, ≤ 0.25 mm tall; gynostegial corona not basally fused into an erect ring that is obscured from view by the faucal annulus.
4. Leaf bases uniformly cuneate; gynostegial stipe edentate; laminar dorsal anther appendages (Cd) slightly emarginate to divergently and sharply bilobed; Jamaica. ________ **7. G. stellatus**
4. Leaf bases cordate; gynostegial stipe with a single tooth borne on lower portion of the column, just above the upwardly rising segment of each Cs; laminar dorsal anther appendages (Cd) truncate or rounded; Cuba, Hispaniola, Puerto Rico ________ **8. G. stephanotrichus**

LESSER ANTILLES

1. Faucal annulus of corolla (corolline corona or Ca) an uninterrupted ring, conspicuously raised (to 0.5 mm tall), pubescent along the entire rim or only opposite each corolla lobe sinus; gynostegial corona appearing densely folded apically, basally fused into a ring, obscured from view by the faucal annulus; gynostegial stipe 1–1.5 mm tall; Cd emarginate; Dominica ________ **9. G. waitukubuliensis**
1. Faucal annulus of corolla (corolline corona or Ca) reduced to an interrupted ridge, distinct only opposite each corolla lobe sinus, tufted pubescent to glabrate or, if uninterrupted, then very shallow, mostly 0.08 mm tall, and glabrous, except to 0.16 mm tall and tufted pubescent opposite each corolla lobe sinus; gynostegial corona neither apically densely folded nor basally obscured by a faucal annulus; gynostegial stipe ≤ 1 mm tall; Cd rounded or truncate (emarginate in *G. absalonensis*).
2. Interstaminal gynostegial corona double (i.e., a narrower upper ligulate corona lobe occurring on top of the broader lower corona–Fig. 6E, 8E).
3. Corolla robust, base of corolla tube subcampanulate, as broad as long or broader than long; horizontal length of lower interstaminal gynostegial corona (Ci) from base of stipe to lobe apex 1.1–1.4 mm, narrow upper ligulate corona lobe of the Ci abruptly ending in a scooped out depression before reaching the stipe base, dorsally ridged; St. Lucia ________ **3. G. iyanolensis**
3. Corolla slender, base of corolla tube elongate-campanulate, distinctly longer than broad; horizontal length of interstaminal gynostegial corona (Ci) from base of stipe to lobe apex ≤ 0.7 mm, narrow upper ligulate corona lobe of the Ci ending essentially at the stipe base, dorsally plane or sometimes slightly raised into a shallow bump; Martinique ________ **5. G. martinicensis**
2. Interstaminal gynostegial corona single.
4. Gynostegial stipe with a single tooth ca. 0.2 mm long below each anther; St. Vincent ________ **10. G. youroumaynensis**
4. Gynostegial stipe edentate.
5. Corolla lobes (10–)12–17 mm long; Cs to 1 mm tall; interstaminal gynostegial corona (Ci) with two distinctly raised and rounded mounds; laminar dorsal anther appendages (Cd) truncate or rounded; Guadeloupe and Martinique ________ **2. G. dussii**
5. Corolla lobes 4.8–6.7 mm long; Cs < 0.3 mm tall; interstaminal gynostegial corona (Ci) smooth, lacking raised bumps; laminar dorsal anther appendages (Cd) rounded bilobed; Martinique ________ **1. G. absalonensis**

1. Gonolobus absalonensis Krings, Syst. Bot. 32:181. 2007. (**Fig. 4**). TYPE: MARTINIQUE: Absalon, Près la cascade, May 1910 (fl), Herb. d'Alleizette *s.n.* [*4801*?] (HOLOTYPE: L!).

Herbaceous perennial vines. Latex unknown, presumably white. Stems glabrate to very sparsely pubescent, both short, capitate-glandular, and longer, sharp, eglandular trichomes present, the latter retrorse internodally and antrorse-appressed along an indistinct, horizontal ridge between two opposite petioles and/or just above the node, to 0.5 mm long; nodes sparsely pubescent, gland field apparently absent. Leaf blades ovate to oblong-ovate, (3.4–)6.6–8.6 cm × (1.3–)3.4–4.5 cm, apices abruptly acuminate with the acumen narrowly obtuse, to 0.7 cm long, bases deeply or shallowly cordate, margins entire, adaxial surface sparsely strigose, abaxial surface more densely strigose with sharp, eglandular trichomes scattered along the major and minor

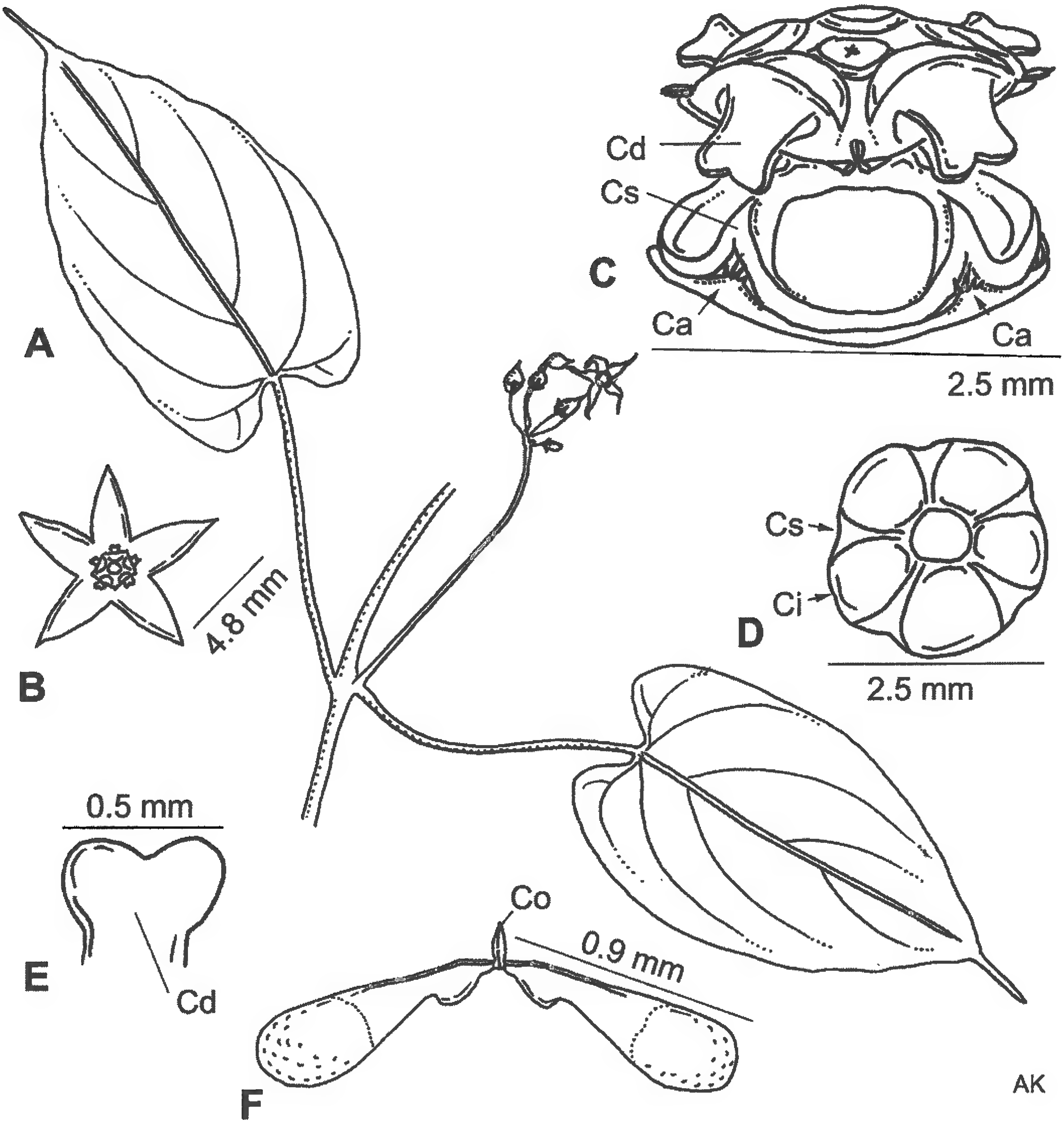

Fig. 4. ***Gonolobus absalonensis*. A.** Leaves and inflorescence. **B.** Open flower. **C.** Faucal annulus of the corolla (Ca), gynostegial corona, and style-head. **D.** Gynostegial corona of fused staminal (Cs) and interstaminal (Ci) segments (style-head removed). **E.** Laminar dorsal anther appendage (Cd). **F.** Pollinarium. Based on Herb. d'Alleizette s.n. [*4801?*] (L). **Ca** = faucal annulus of corolla; **Ci** = interstaminal gynostegial corona segment; **Cd** = laminar dorsal anther appendage; **Co** = corpusculum; **Cs** = staminal gynostegial corona segment.

veins, colleters 2, 0.5–0.9 mm long; petioles 3.6–5.7 cm long, glabrous or very sparsely pubescent on all sides, capitate trichomes to 0.1 mm long, sharp, eglandular trichomes ca. 0.3 mm long, antrorsely-appressed or -ascending; stipular colleters 2, ca. 0.3 mm long, one borne on each side of the petiole base. Inflorescences racemiform, peduncles 4.1–5.4 cm long, glabrate to very sparsely pubescent, capitate, as well as sharp, eglandular trichomes present, the latter antrorsely-appressed or –ascending, found primarily at the apex, ca. 0.3 mm long; pedicels 1.5–1.7 cm long, more pubescent at the apex than at the base, capitate-glandular trichomes ca. 0.05 mm long, longer, sharp, eglandular trichomes antrorsely-appressed or –ascending, ca. 0.13 mm long, bracts linear-lanceolate, ca. 0.9 mm × 0.21 mm long, caducous, adaxial surface glabrous, abaxial surface coarsely pubescent, trichomes sharp, eglandular, ca. 0.26 mm long, antrorse. Calyx lobes 5,

lanceolate, 1.95 mm x 1 mm, apices narrowly obtuse or acute, margins glabrous, abaxial surface pubescent mostly at the base, sharp, eglandular trichomes, antrorsely-ascending or -appressed, to 0.25 mm long; colleters 1 per sinus. Corolla lobes 5, lanceolate to ovate, 4.8–6.7 mm x 2.5–2.8 mm, slightly lobed at the base, a glandular swelling frequently present in the sinus, adaxial glabrous, abaxial surface glabrous; faucal annulus (corolline corona or Ca) a shallow, uninterrupted ring, ca. 2.5 mm diam, ca. 0.08 mm tall, glabrous except where raised opposite each corolla lobe sinus, then to ca. 0.16 mm tall and short hispid; gynostegial corona of fused staminal (Cs) and interstaminal parts (Ci), single, 5-lobed, erect- or prostrate-undulating, 0.4–0.6 mm tall; anther guiderails without appendages; laminar dorsal anther appendages (Cd) 0.48–0.7 mm x 0.5–0.8 mm, emarginate; style-head ca. 3.2 mm diam, stipe 0.3–0.5 mm long, not toothed. Pollinaria: corpuscula ca. 0.18 mm long, pollinia borne horizontally, ovate, ca. 0.9 mm x 0.3 mm. Follicles unknown.

Phenology.—Flowering in May.

Distribution.—*Gonolobus absalonensis* is endemic to Martinique (Fig. 1). Its habitat is poorly known, but likely primarily middle elevation rainforest based on the requirements of most congenerics in the Lesser Antilles. The type was apparently collected near a waterfall.

Provisional conservation status.—IUCN: Critically endangered (CR)—B1a,biii. NatureServe: GH NH.

Taxon concept mapping.— < *G. martinicensis* sensu Duss (1897); < *G. martinicensis* sensu Schlechter (1899); < *G. martinicensis* sensu Howard (1988); < *G. martinicensis* sensu Fournet (2002).

Notes.—*Gonolobus absalonensis* is the smallest-flowered Lesser Antillean *Gonolobus* species (corolla lobes reaching only to 6.7 mm) and one of three *Gonolobus* species known from Martinique. It can be distinguished from other *Gonolobus* species on Martinique by the following key:

1. Corolla lobes to 6.7 mm long, both surfaces glabrous; interstaminal gynostegial corona (Ci) single, smooth, lacking raised bumps; laminar dorsal anther appendages (Cd) emarginate ____ **1. G. absalonensis**
1. Corolla lobes > 9.5 mm long, either or both surfaces pubescent; interstaminal gynostegial corona (Ci) double or if single, then with defined raised bumps medially; laminar dorsal anther appendages (Cd) rounded or truncate.
    2. Interstaminal gynostegial corona single ____ **2. G. dussii**
    2. Interstaminal gynostegial corona double (i.e., a narrower upper ligulate corona lobe occurring on top of the broader lower corona) ____ **5. G. martinicensis**

2. Gonolobus dussii Krings, Syst. Bot. 32:183. 2007. (**Fig. 5**). TYPE: GUADELOUPE: Chemin de la Soufrière, alt. 500 m, s.d. (fl), *Quentin 732* (HOLOTYPE: P!; ISOTYPE: GH!).

Herbaceous perennial vines. Latex unknown, presumably white. Stems glabrate to very sparsely pubescent, both short, capitate-glandular, and longer, sharp, eglandular trichomes present, the latter retrorse internodally, and antrorse-appressed along an indistinct, horizontal ridge between two opposing petioles and/or just above the node, to 0.5 mm long; nodes pubescent or glabrous, gland field apparently absent. Leaf blades ovate to oblong-ovate, (3.3–)5.7–10.7 cm x (0.9–)2.5–6.1 cm, apices gradually acuminate with the acumen narrowly obtuse, to 2 cm long, bases deeply or shallowly cordate, margins entire, adaxial surface glabrate or sparsely strigose, abaxial surface glabrate or more densely strigose with sharp, eglandular trichomes scattered along the major and minor veins, colleters 2–3, 0.4–0.6 mm long; petioles (1.3–)2.1–5.5 cm long, glabrous or sparsely pubescent on all sides, capitate trichomes to 0.09 mm long, sharp, eglandular trichomes 0.3–0.4 mm long, mostly antrorsely appressed or ascending (some spreading and a very few retrorse); stipular colleters 2, ca. 0.3 mm long, one borne on each side of the petiole base. Inflorescences racemiform, peduncles 0.7–2.3 cm long, glabrate to very sparsely pubescent, capitate, as well as sharp, eglandular trichomes present, the latter antrorsely-appressed or -ascending, found primarily at the apex, ca. 0.3 mm long; pedicels 1.8–2.2 cm long, more pubescent at the apex than at the base, capitate-glandular trichomes ca. 0.08 mm long, longer sharp, eglandular trichomes antrorsely-appressed or -ascending, ca. 0.3 mm long, bracts linear-lanceolate, ca. 1.5 mm x 0.17 mm long, caducous, adaxial surface glabrous, abaxial surface coarsely pubescent, trichomes sharp, eglandular, ca. 0.2 mm long, antrorse. Calyx lobes 5, sublanceolate to elongate triangular (widest at or just above the base), 3.9–5.8 mm x 1–1.5 mm, apices obtuse to narrowly rounded, margins glabrous, abaxial surface coarsely pubescent at the base and variously toward the apex, trichomes antrorsely-appressed or

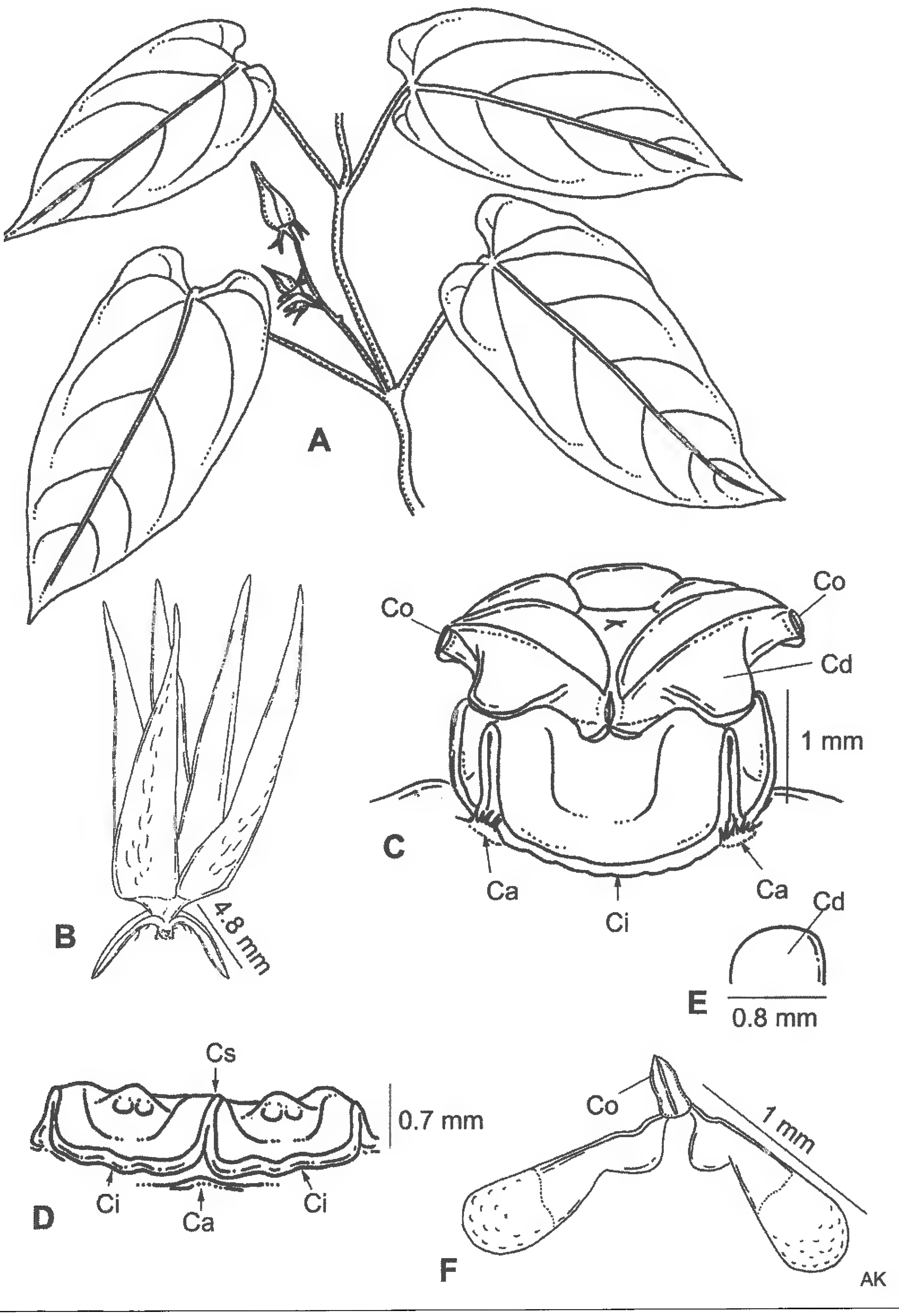

FIG. 5. *Gonolobus dussii*. **A.** Leaves and inflorescence. **B.** Flower showing coarse abaxial pubescence of the corolla lobes. **C.** Faucal annulus of the corolla (Ca), gynostegial corona, and style-head. **D.** Gynostegial corona of fused staminal (Cs) and interstaminal (Ci) segments (style-head removed). **E.** Laminar dorsal anther appendage (Cd). **F.** Pollinarium. A–B based on *Duss 3775* (NY). C and E–F based on *Duss 4565* (NY). D based on *Quentin 732* (P). **Ca** = faucal annulus of corolla; **Ci** = interstaminal gynostegial corona segment; **Cd** = laminar dorsal anther appendage; **Co** = corpusculum; **Cs** = staminal gynostegial corona segment.

-ascending, to 0.5 mm long; colleters 1 per sinus. Corolla lobes 5, narrowly lanceolate to elongate triangular, (10–)12–17 mm x 3.2–3.7 mm, slightly overlapping at the base, a glandular swelling frequently present in the sinus, adaxial surface glabrous, abaxial surface with coarse, sharp, eglandular trichomes, antrorsely-appressed or -ascending, particularly at the base and variously toward the apex, ca. 0.36 mm long; faucal annulus (corolline corona or Ca) interrupted, a distinctly raised ridge opposite each corolla lobe sinus, short-hispid or glabrate; gynostegial corona of fused staminal (Cs) and interstaminal parts (Ci), single, erect-undulating, two distinctly raised and rounded mounds borne in the interstaminal position; anther guiderails without appendages, laminar dorsal anther appendages (Cd) ca. 0.8 mm wide, rounded or emarginate; style-head 2.3–2.4 mm diam, stipe ca. 0.45 mm long, not toothed. Pollinaria: corpuscula 0.18–0.3 mm long, pollinia borne horizontally, ovate, ca. 0.5–1 mm x 0.25–0.35 mm. Follicles unknown.

Phenology.—Flowering in April, June, and October.

Distribution.—*Gonolobus dussii* occurs in Guadeloupe and Martinique (Fig. 1). Its habitat is not well known, but it appears to have been collected from riversides and at mid-elevations (480–500 m).

Provisional conservation status.—IUCN: Critically endangered (CR)—B1a,biii. NatureServe: Guadeloupe (GH NH); Martinique (GH NH).

Taxon concept mapping.— < *G. martinicensis* sensu Duss (1897); < *G. martinicensis* sensu Schlechter (1899); < *G. martinicensis* sensu Howard (1988); < *G. martinicensis* sensu Fournet (2002).

Notes.—*Gonolobus dussii* can be distinguished from *G. youroumaynensis* of St. Vincent by the short pedicel trichomes, the edentate stipe, and the adaxially glabrous corolla lobes. The gynostegial coronas of *G. absalonensis*, *G. dussii*, and *G. youroumaynensis* are most similar to each other among Lesser Antillean *Gonolobus* species, but *G. dussii* uniquely exhibits two distinctly raised and rounded mounds in the interstaminal position (Fig. 5). The mounds appear very close and near ridge-like in Martinique specimens, as well as *Duss 3775* of Guadeloupe. Additional collections are needed to determine the extent of variation in the coronas and to evaluate whether additional taxa are represented.

Additional specimens examined. **GUADELOUPE:** Bord de la riviere Noire, 29 Jun 1895 (fl), *Duss 3775* (MO-fragment, NY); Pointe-Noire, 20 Oct 1895 (fl), *Duss 3714* (NY-2 sheets). **MARTINIQUE:** Environs a St. Pierre, 1884 (fl), *Duss "1862, 4565"* (NY); Pointe-Fine, près de la riviere Calabre, Apr 1900 (fl), *Duss 4565* (NY).

3. Gonolobus iyanolensis Krings, Syst. Bot. 32:185. 2007. **(Fig. 6).** Type: ST. LUCIA: Gros Piton, 9 Aug 1996 ["9/8/76"] (fl), *Graveson 107* (holotype: GH!).

Herbaceous perennial vines. Latex white. Stems glabrous or glabrate, both short, capitate-glandular, and longer, sharp, eglandular trichomes present, the latter retrorse or spreading internodally, and antrorse-appressed along an indistinct, horizontal ridge between two opposing petioles, to 1.2 mm long; nodes pubescent or glabrous in age, gland field sometimes present. Leaf blades ovate to oblong-ovate, to 8 cm x 5.4 cm, apices obtuse or short-acuminate with the acumen obtuse, bases cordate, margins entire, adaxial surface glabrous, abaxial surface glabrous or with sharp, eglandular trichomes scattered along the major veins, colleters 2–4, 0.37-0.65 mm long; petioles to 6.2 cm long, glabrous or glabrate, capitate-glandular trichomes very sparse if present, sharp, eglandular trichomes near apex if present, to 0.9 mm long; stipular colleters 2, ca. 0.3 mm long, one borne on each side of the petiole base. Inflorescences racemiform, peduncles 2.1–2.8 cm long, glabrous or glabrate, sharp, eglandular hairs antrorsely-appressed or -ascending, most pronounced near apex, ca. 0.7 mm long; pedicels 2.8–3.1 cm long, glabrate, capitate-glandular trichomes scattered throughout or only near the apex, ca. 0.09 mm long, longer, sharp, eglandular hairs antrorsely- appressed or -ascending, occurring only near the apex, 0.3-0.9 mm long, bracts linear-lanceolate, ca. 2.8 mm x 0.5 mm long, caducous, adaxial surface glabrous, abaxial surface coarsely pubescent, trichomes sharp, eglandular, ca. 0.4 mm long, antrorse. Calyx lobes 5, lanceolate (widest distinctly above the base, ca. 1.5–2 mm above base), 6.1–6.6 mm x 1.6–1.8 mm, apices obtuse, margins glabrous, abaxial surface glabrous or glabrate with the few trichomes present, coarse, antrorsely-ascending or -appressed, to 0.4 mm long; colleters 1 per sinus. Corolla lobes 5, lanceolate, 10.2–17.3 mm x 2.7–4.8 mm, slightly lobed at the base, a glandular swelling frequently present in the sinus, adaxial surface pubescent along the right half, trichomes flat, ribbon-like,

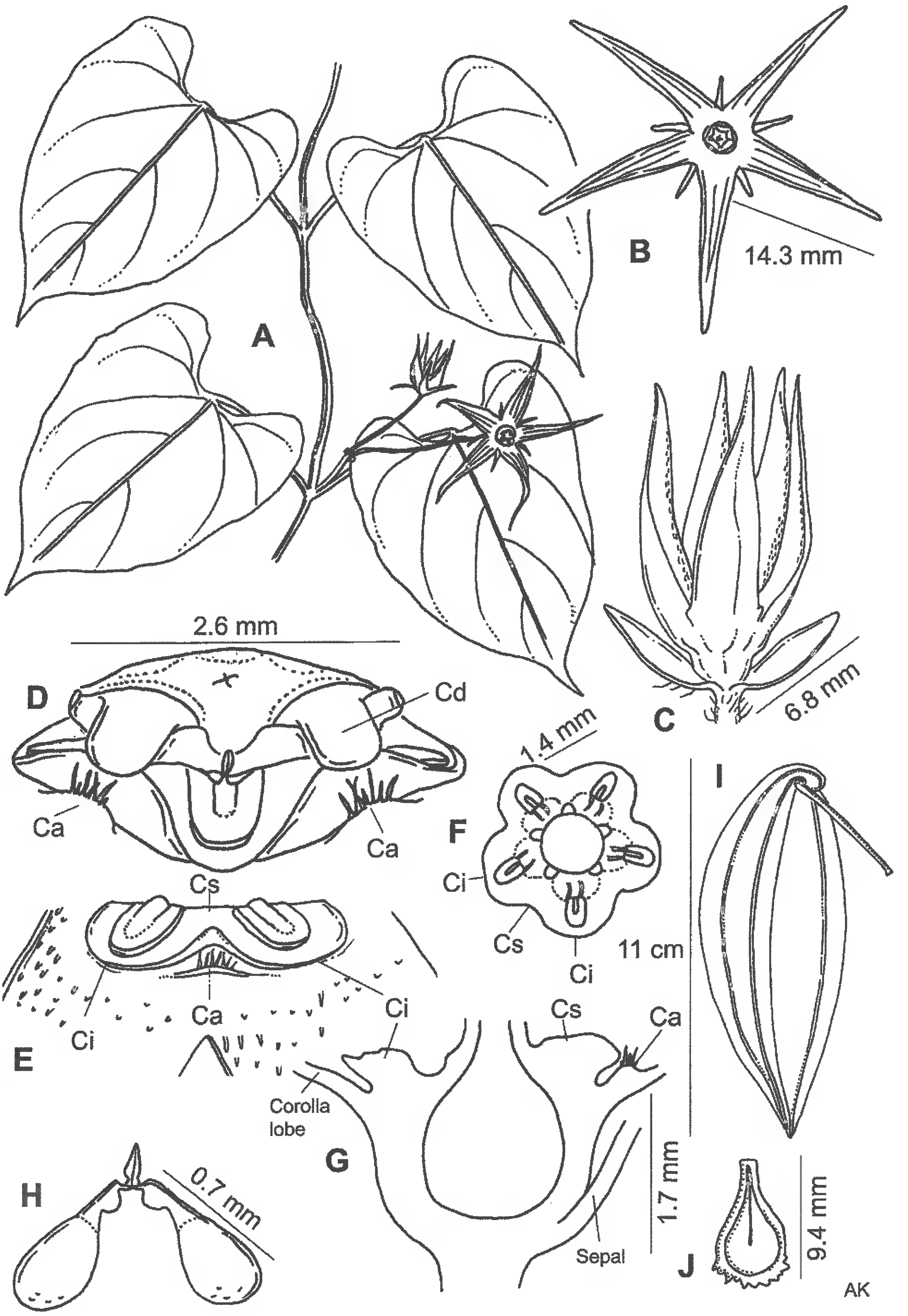

Fig. 6. *Gonolobus iyanolensis*. **A.** Leaves and inflorescence. **B.** Open flower. **C.** Flower showing adaxial pubescence of the corolla lobes. **D.** Faucal annulus of the corolla (Ca), gynostegial corona, and style-head. **E.** Gynostegial corona of fused staminal (Cs) and interstaminal (Ci) segments (style-head removed), showing dorsal ridge of upper ligulate corona lobe of the Ci. **F.** Top view of gynostegial corona (style-head removed). **G.** Cross-section of corolla tube showing position of corollar and gynostegial corona elements. **H.** Pollinarium. **I.** Follicle. **J.** Seed. A–B based on *Johnny 57 et al.* (UPRRP). C and E based on *Graveson 107* (GH). D and F–H based on *Krings 1373 et al.* (NCSC). I–J based on *Graveson s.n.* (NCSC). **Ca** = faucal annulus of corolla; **Ci** = interstaminal gynostegial corona segment; **Cd** = laminar dorsal anther appendage; **Co** = corpusculum; **Cs** = staminal gynostegial corona segment.

0.18–0.26 mm long, abaxial surface glabrous; faucal annulus (corolline corona or Ca) interrupted, a distinctly raised ridge, opposite each corolla lobe sinus, short hispid; gynostegial corona of fused staminal (Cs) and interstaminal parts (Ci), double, 5-lobed, prostrate, narrow upper ligulate corona lobe of the Ci appressed to the lower, abruptly ending in a scooped out depression before reaching the stipe base (horizontal length of lower interstaminal gynostegial corona (Ci) from base of stipe to lobe apex 1.1–1.4 mm), dorsally ridged; anther guiderails apparently without appendages, laminar dorsal anther appendages (Cd) 0.5–0.6 mm wide, rounded or truncate; style-head ca. 2.5 mm diam, stipe ca. 0.23 mm long, not toothed. Pollinaria: corpuscula 0.16–0.18 mm long, pollinia borne horizontally, ovate, ca. 0.5–0.7 mm × 0.25–0.35 mm. Follicles ovoid, 10–11.6 cm × 3.3–4 cm, 5-winged, appearing glabrous, but with minute papillae or capitate trichomes evident at high magnification; seeds pyriform, compressed, not plano-convex, 8.8–10.5 mm × 4.2–5.9 mm, glabrous, margins dentate, coma to 3.7 cm long.

Phenology.—Flowering in March, July, August, and September. Fruiting in January.

Distribution.—*Gonolobus iyanolensis* is apparently endemic to St. Lucia (Fig. 1), occurring in seasonal deciduous woods from 180–400 m in elevation. An established population occurs on Gros Piton. Roger Graveson (pers. comm.) noted having seen vines away from the Pitons, but that they have not established themselves well. Woodland boundaries and recent forest openings appear to be the prefered habitat.

Provisional conservation status.—IUCN: Endangered (EN)—B1a,biii. NatureServe: G1 N1.

Taxon concept mapping.— < *G. martinicensis* sensu Schlechter (1899); < *G. martinicensis* sensu Howard (1988).

Notes.—Roger Graveson (pers. comm.) noted that the collection date is incorrect on the label of his collection *Graveson 107* (GH) and should instead be 9 Aug 1996. *Gonolobus iyanolensis* is immediately recognizable among Lesser Antillean *Gonolobus* species by its double interstaminal gynostegial corona (Ci). The only other species that shares this corona type in the area is *G. martinicensis*. (Fig. 8). In contrast to the robust-flowered *G. iyanolensis*, *G. martinicensis* exhibits distinctly more slender flowers with elongate-campanulate bases (ca. 2 mm long) that are longer than wide (as wide as long or wider than long in *G. iyanolensis*) and a narrower gynostegial corona (see key). The distinct dorsal ridge of the narrow upper ligulate corona lobe of the Ci in *G. iyanolensis* has also not been seen in *G. martinicensis*, which is either plane in the homologous position or exhibits a slightly raised bump.

Additional specimens examined. **ST. LUCIA:** Chassin, edge of clearing, 7 Jan 1987 (fr), *Slane 1056* (GH); Soufrière, Gros Piton summit, facing Soufrière, 5 Jul 2005 (fl), *Johnny 57 with Samuel and Sealys* (UPRRP); Soufrière, Gros Piton summit, facing Soufrière, 13 Sep 2005 (fl), *Graveson 1248 with Smith* (UPRRP); Gros Piton, 11 Mar 2006 (fl), *Krings 1373 with Graveson and Smith* (NCSC).

4. Gonolobus jamaicensis Rendle, J. Bot. 74:345. 1936. (**Fig. 7**). TYPE: JAMAICA: near Vinegar Hill, climbing up trees to height of 20 ft, 4200 ft elev., 5 Jun 1896 (fl), *Harris 6368* (HOLOTYPE: BM!).

Herbaceous perennial vines. Latex white. Stems pubescent, both short, capitate-glandular, and longer, sharp, eglandular trichomes present, the latter spreading or retrorse internodally, and antrorse-appressed along an indistinct, horizontal ridge between two opposing petioles and/or just above the node, to 1.8 mm long; nodes pubescent, gland field apparently absent. Leaf blades elliptic to ovate, (2–)3.9–9.7 cm × (1.3–)1.8–6.6 cm, apices acuminate, acumen narrowly obtuse, to 1.1 cm long, bases cuneate, rounded, truncate, or cordate (frequently all base types present on a single individual vine), margins entire, adaxial surface glabrate, abaxial surface sparsely pubescent to glabrate, sharp, eglandular trichomes relatively dense along the major and minor veins, colleters 2, ca. 0.45 mm long; petioles 0.9–3.5 cm long, pubescent on all sides, capitate trichomes to 0.13 mm long, sharp, eglandular trichomes ca. 1.25 mm long, mostly spreading or retrorse, less dense than the capitate trichomes; stipular colleters 2, ca. 0.29 mm long, one borne on each side of the petiole base. Inflorescences racemiform, peduncles to 4.3 cm long, pubescent, capitate, as well as sharp, eglandular trichomes present, the latter spreading, retrorse, or antrorsely-ascending or –appressed, ca. 0.5 mm long; pedicels 1.2–1.4 cm long, evenly pubescent throughout, capitate-glandular trichomes ca. 0.08 mm long, longer sharp, eglandular trichomes antrorsely-appressed or -ascending, ca. 0.4 mm long, bracts linear-lanceolate, ca. 1.7 mm × 0.5 mm long, caducous, adaxial surface glabrous, abaxial surface coarsely

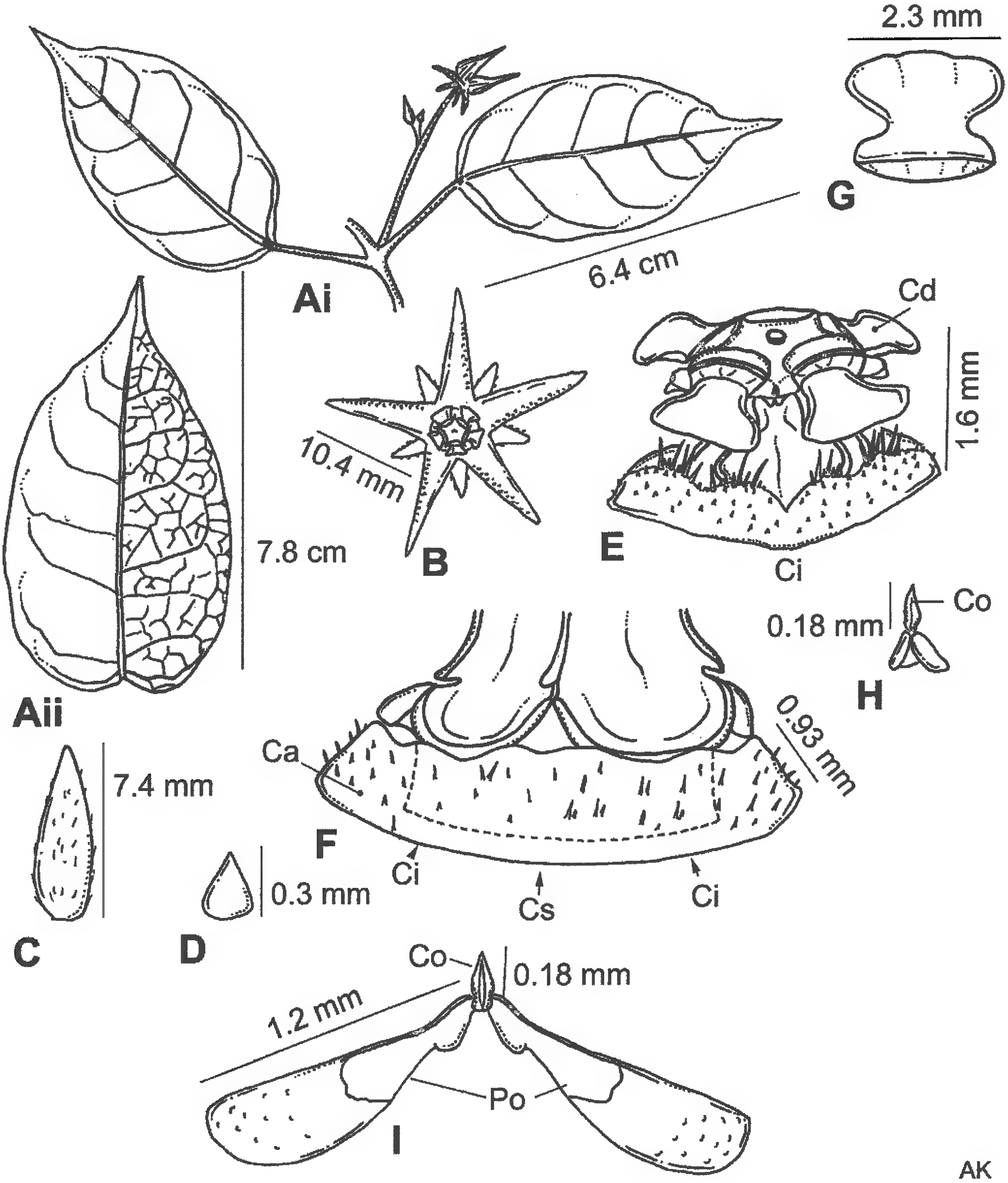

Fig. 7. ***Gonolobus jamaicensis*****. Ai–ii. Leaves and inflorescence. B. Open flower. C. Sepal. D. Calycine colleter. E. Faucal annulus of the corolla, gynostegial corona, and style-head. F. Detail of faucal annulus and base of gystegial stipe. G. Laminar dorsal anther appendage. H. Corpusculum and subtending anther wings. I. Pollinarium. Ai–I based on *Kelly et al. 10207* (TCD). Aii based on *Proctor 6828* (GH). Ca = faucal annulus of corolla; Ci = interstaminal gynostegial corona segment; Cd = laminar dorsal anther appendage; Co = corpusculum; Cs = staminal gynostegial corona segment; Po = pollinium.**

pubescent, trichomes sharp, eglandular, ca. 0.3 mm long, antrorse. Calyx lobes 5, lanceolate, 4.3–7.45 mm × 1.6–2.2 mm, apices obtuse, margins glabrous or sparsely ciliolate, abaxial surface pubescent at the base and glabrous toward the apex, trichomes antrorsely-appressed, largest to 0.5 mm long; colleters 1 per sinus. Corolla lobes 5, lanceolate, 10–13 mm × 3.8–5 mm, slightly overlapping at the base, a glandular swelling frequently present in the sinus, adaxial surface pubescent along the right, abaxial surface glabrous; faucal

annulus (corolline corona or Ca) a continuous ring, bilobed opposite each anther, ca. 0.93 mm tall, short-pubescent and papillate throughout; gynostegial corona of fused staminal (Cs) and interstaminal parts (Ci), single, erect-undulating, interstaminal secondary nectaries apparently absent or at least not formed into conspicuous bumps or mounds; anther guiderails without appendages, laminar dorsal anther appendages (Cd), ca. 2.3 × 1.7 mm, spreading, apices truncate; style-head ca. 3.3 mm diam, stipe ca. 1 mm long, dentate, teeth appearing as notches, borne on the lower portion of the column, just above the upwardly rising segment of each Cs. Pollinaria: corpuscula ca. 0.18 mm long, pollinia borne horizontally, ovate, ca. 1.2 mm × 0.3 mm. Follicles unknown.

Phenology.—Flowering in March and June.

Distribution.—*Gonolobus jamaicensis* is endemic to Jamaica. It is known only from montane rainforests from 1025–1200 m elevation.

Provisional conservation status.—IUCN: Vulnerable (VU)—B1a,c. NatureServe: G3 N3.

Taxon concept mapping.— = *G. rostratus* sensu Schlechter (1899); = *G. jamaicensis* sensu Adams (1972).

Notes.—*Gonolobus jamaicensis* was proposed by Rendle (loc. cit.) as a *nomen novum* for the Jamaican endemic taxon Schlechter (1899) treated as *G. rostratus* (Vahl) R.Br. Not only did Robert Brown never make the combination attributed to him (see Mem. Wernerian Nat. Hist. Soc. 1:35. 1810), but the true *Gonolobus rostratus* (Vahl) Schult. is only known from Trinidad (and perhaps South America). It is based on the type of *Cynanchum rostratum* Vahl. Because Rendle corrected a misapplication, his name—*G. jamaicensis*—is a new species name, not a *nomen novum* as he mistakenly stated. A *nomen novum* is an avowed substitute (replacement name) for a validly published but illegitimate name, the type of which would be the same as that of the name which it replaced.

Additional specimens examined. **JAMAICA:** 1886 (fl), *Hart 968* (MO [2 single leaves and 2 flowers]; US); John Crow Mountains, eastern Jamaica, SE of Millbank, 17 Mar 1992 (fl), *Kelly, Iremonger and REA team 10207* (TCD). **Portland Parish:** 0.5 mi N of Hardwar Gap, near the waterfall, 22 Jun 1952 (fl), *Proctor 6828* (A, IJ); 0.5 mi N of Hardwar Gap, uphill from the trail above the "Waterfall," 3 Mar 2006 (st), *Krings 1393 with Suiter and Proctor* (IJ, NCSC).

5. Gonolobus martinicensis Decne. in DC., Prodr. 8:595. 1844. (**Fig. 8**). TYPE: MARTINIQUE: s.d. (fl), *Pleé s.n.* (LECTOTYPE, designated by Krings 2007: P!).

"*Gonolobus scandens* (Aubl.) Urb.," Repert. Spec. Nov. Regni Veg. 16:151. 1919, nom. illeg. (see Nicolson 1991).

Herbaceous perennial vines. Latex unknown, presumably white. Stems villous to glabrate, both short, capitate-glandular, and longer, sharp, eglandular trichomes present, the latter retrorse or spreading internodally, and antrorse-appressed along an indistinct, horizontal ridge between two opposing petioles, to 1.9 mm long; nodes pubescent or glabrous in age, gland fields sometimes present. Leaf blades ovate to oblong-ovate, to 6.4 cm × 4.9 cm, apices obtuse, gradually to abruptly acuminate with the acumen to 1.4 cm long, bases cordate, margins entire, adaxial surface sparsely strigillose, abaxial surface pubescent along the veins, trichomes strigillose (and longer, sharp, eglandular, scattered particularly along the midvein), colleters 2, 0.7 mm long; petioles to 4 cm long, villous, capitate-glandular trichomes sparse but throughout, sharp, eglandular trichomes ubiquitous, mostly antrorse-ascending and spreading, to 1 mm long; stipular colleters 2, ca. 0.24 mm long, one borne on each side of the petiole base. Inflorescences racemiform, peduncles 1.5–2.1 cm long, villous with sharp, eglandular hairs antrorsely- or retrorsely -appressed or –ascending/-descending and spreading, ca. 0.44 mm long, capitate trichomes throughout; pedicels to 1.9 cm long, less pubescent than peduncles, capitate-glandular trichomes throughout, ca. 0.09 mm long, longer, sharp, eglandular hairs antrorsely- appressed or -ascending, throughout, though most dense at the apex, ca. 0.47 mm long, bracts linear-lanceolate, ca. 1.6 mm × 0.17 mm long, caducous, adaxial surface glabrous, abaxial surface coarsely pubescent, trichomes sharp, eglandular, ca. 0.2 mm long, antrorse. Calyx lobes 5, oblong lanceolate, 4.5–5 mm × 0.8 mm, apices obtuse or acute, margins sparsely ciliolate, abaxial surface glabrate with the few trichomes present, coarse, antrorsely-ascending or -appressed, to 0.3 mm long; colleters 1 per sinus. Corolla lobes 5, lanceolate, 9.7–11.4 mm × 2–3.5 mm, slightly lobed at the base, a glandular swelling frequently present in the sinus, adaxial surface pubescent along the right half, trichomes flat, ribbon-like, ca. 0.2 mm long, abaxial

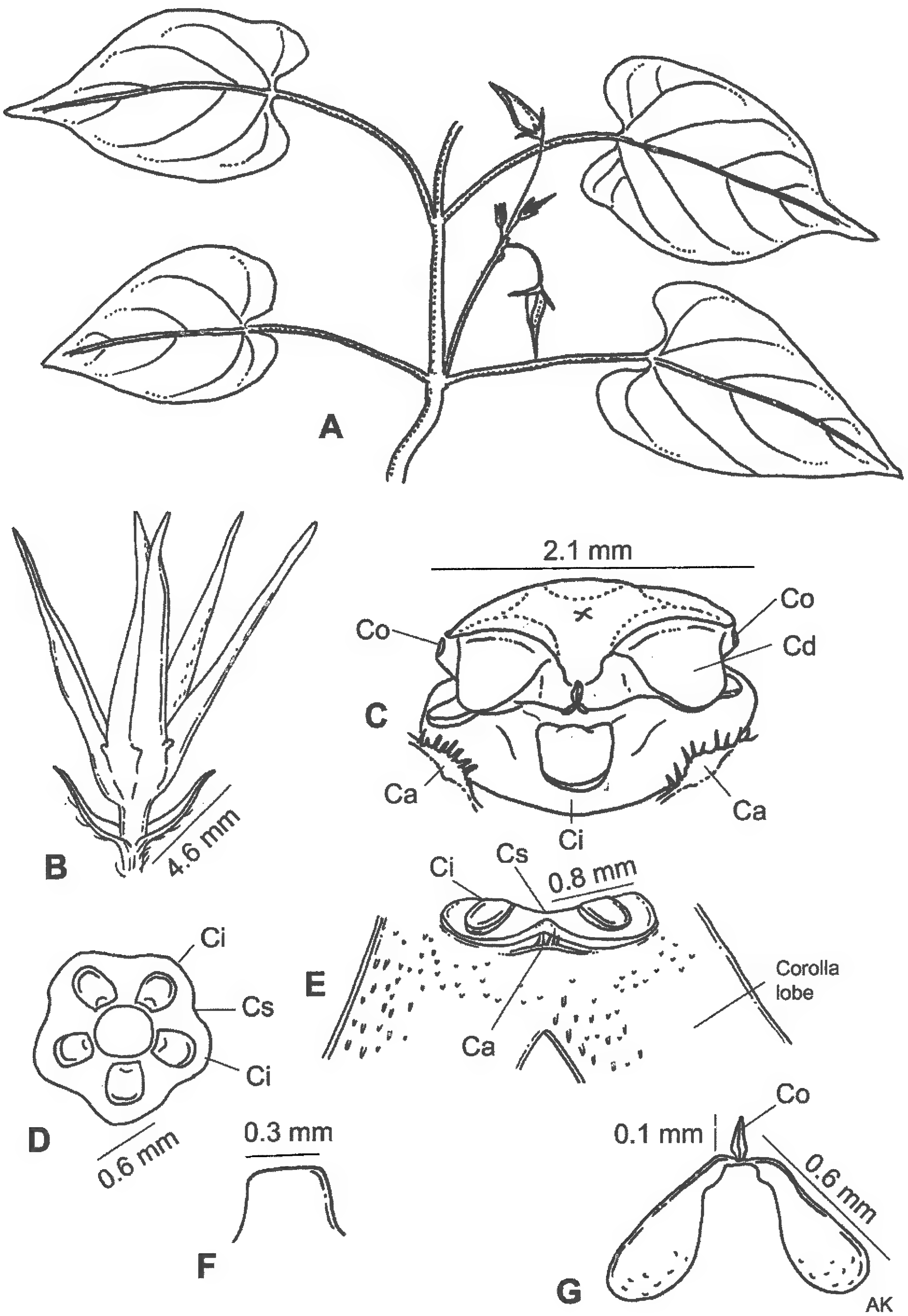

FIG. 8. *Gonolobus martinicensis*. **A.** Leaves and inflorescence. **B.** Flower showing narrow corolla tube. **C.** Faucal annulus (Ca), gynostegial corona, and style-head. **D.** Top view of gynostegial corona (style-head removed). **E.** Gynostegial corona of fused staminal (Cs) and interstaminal (Ci) segments (style-head removed), showing upper ligulate corona lobe of the Ci. **F.** Laminar dorsal anther appendage (Cd). **G.** Pollinarium. A based on Herb. Mart. Suppl. Nr. 63 (MO). B and E–F based on *Lieber s.n.* (M). C–D and G based on L.C. Rich. Herb. Guyanensi-Antillanum (P). **Ca** = faucal annulus of corolla; **Ci** = interstaminal gynostegial corona segment; **Cd** = laminar dorsal anther appendage; **Co** = corpusculum; **Cs** = staminal gynostegial corona segment.

surface glabrate with a few, sparse, sharp, eglandular trichomes near the base, middle, and margin along the tip; faucal annulus (corolline corona or Ca) interrupted, a distinctly raised ridge, opposite each corolla lobe sinus, short hispid; gynostegial corona of fused staminal (Cs) and interstaminal parts (Ci), double, 5-lobed, prostrate, narrow upper ligulate corona lobe of the Ci appressed to the lower, ending essentially at the stipe base (horizontal length of interstaminal gynostegial corona (Ci) from base of stipe to lobe apex ≤ 0.7 mm), dorsally plane or sometimes raised into a shallow bump; anther guiderails apparently without appendages, laminar dorsal anther appendages (Cd) 0.2 mm wide, rounded or truncate; style-head 1.8–2.3 mm diam, stipe ca. 0.28 mm long, not toothed. Pollinaria: corpuscula 0.1–0.15 mm long, pollinia borne horizontally, ovate, 0.45–0.6 mm × 0.24-0.26 mm. Follicles unknown.

Phenology.—The months of flowering are unknown.

Distribution.—*Gonolobus martinicensis* is apparently endemic to Martinique (Fig. 1). Its habitat is unknown, but likely primarily middle elevation rainforest based on the requirements of most congenerics in the Lesser Antilles.

Provisional conservation status.—IUCN: Critically endangered (CR)—B1a,biii. NatureServe: GH NH.

Taxon concept mapping.— < *G. martinicensis* sensu Duss (1897); < *G. martinicensis* sensu Schlechter (1899); < *G. martinicensis* sensu Howard (1988); *G. martinicensis* sensu Fournet (2002).

Notes.—*Gonolobus martinicensis* is immediately recognizable among Lesser Antillean *Gonolobus* species by its double (or ligulate) interstaminal gynostegial corona (Ci). The only other species that shares this corona type in the area is *G. iyanolensis*. (Fig. 6). In contrast to the robust-flowered *G. iyanolensis*, *G. martinicensis* exhibits distinctly more slender flowers with elongate-campanulate bases (ca. 2 mm long) that are longer than wide (as wide as long or wider than long in *G. iyanolensis*) and a narrower gynostegial corona (see key). The distinct dorsal ridge of the narrow upper ligulate corona lobe of the Ci in *G. iyanolensis* has also not been seen in *G. martinicensis*, which is either plane in the homologous position or exhibits a slightly raised bump.

Additional specimens examined. **MARTINIQUE:** L.C. Rich. Herb. Guyanensi-Antillanum, s.d. (fl) (P-2 specimens [*G. caribaeus* Rich., nom. sched.]); s.d. (fl), *Lieber s.n.* (M).

6. Gonolobus stapelioides Desv. ex Ham., Prodr. Pl. Ind. Occid. 32. 1825. (**Fig. 9**). Type: JAMAICA. Portland Parish: 0.5 mi N of Hardwar Gap, uphill from the trail above the "Waterfall," ca. 3900 ft, montane rainforest, vines growing over trailside shrubs and in small forest openings, population J1, 3 Mar 2006 (fl), *Krings 1395 with Suiter and Proctor* (neotype, here designated: P!; isoneotypes: BM!, IJ!, NCSC!, NY!).

Fischeria cincta Griseb., Fl. Brit. W.I. 421. 1862.
Gonolobus cinctus (Griseb.) Benth. & Hook. f. ex B.D. Jacks., Index Kewensis 1:1054. 1895. Type: JAMAICA: *Higson s.n.* (holotype: K!)

Herbaceous perennial vines. Latex white. Stems pubescent, both short, capitate-glandular, and longer, sharp, eglandular trichomes present, the latter retrorse internodally, and antrorse-appressed along an indistinct, horizontal ridge between two opposing petioles and/or just above the node, to 1.3 mm long; nodes pubescent, gland field apparently absent. Leaf blades elliptic to ovate, 3–9 cm × 1.2–4.5 cm, apices acute or gradually acuminate with the acumen narrowly obtuse, to 0.75 cm long, bases cuneate, rounded, or truncate (frequently all base types present on a single individual vine), margins entire, adaxial surface sparsely strigose, abaxial surface sparsely pubescent to glabrate, sharp, eglandular trichomes relatively dense along the major and minor veins, colleters 2(–3?), ca. 0.5 mm long; petioles 1–2.3 cm long, pubescent on all sides, capitate trichomes to 0.06 mm long, sharp, eglandular trichomes ca. 1.1 mm long, mostly spreading or somewhat retrorse, less dense than the capitate trichomes; stipular colleters 2, ca. 0.3 mm long, one borne on each side of the petiole base. Inflorescences racemiform, peduncles to 2.5 cm long, pubescent, capitate, as well as sharp, eglandular trichomes present, the latter spreading or retrorse, ca. 0.6 mm long; pedicels to 2.5 cm long, pubescent throughout, capitate-glandular trichomes ca. 0.05 mm long, longer sharp, eglandular trichomes spreading or antrorsely-appressed or -ascending, ca. 0.5 mm long, bracts linear-lanceolate, 2.8–3.7 mm × 0.45–0.5 mm long, caducous, adaxial surface glabrous, abaxial surface coarsely pubescent, trichomes sharp, eglandular, 0.36–0.4 mm long, antrorse. Calyx lobes 5, linear-lanceolate, 7–8.5 mm × 2–2.3 mm,

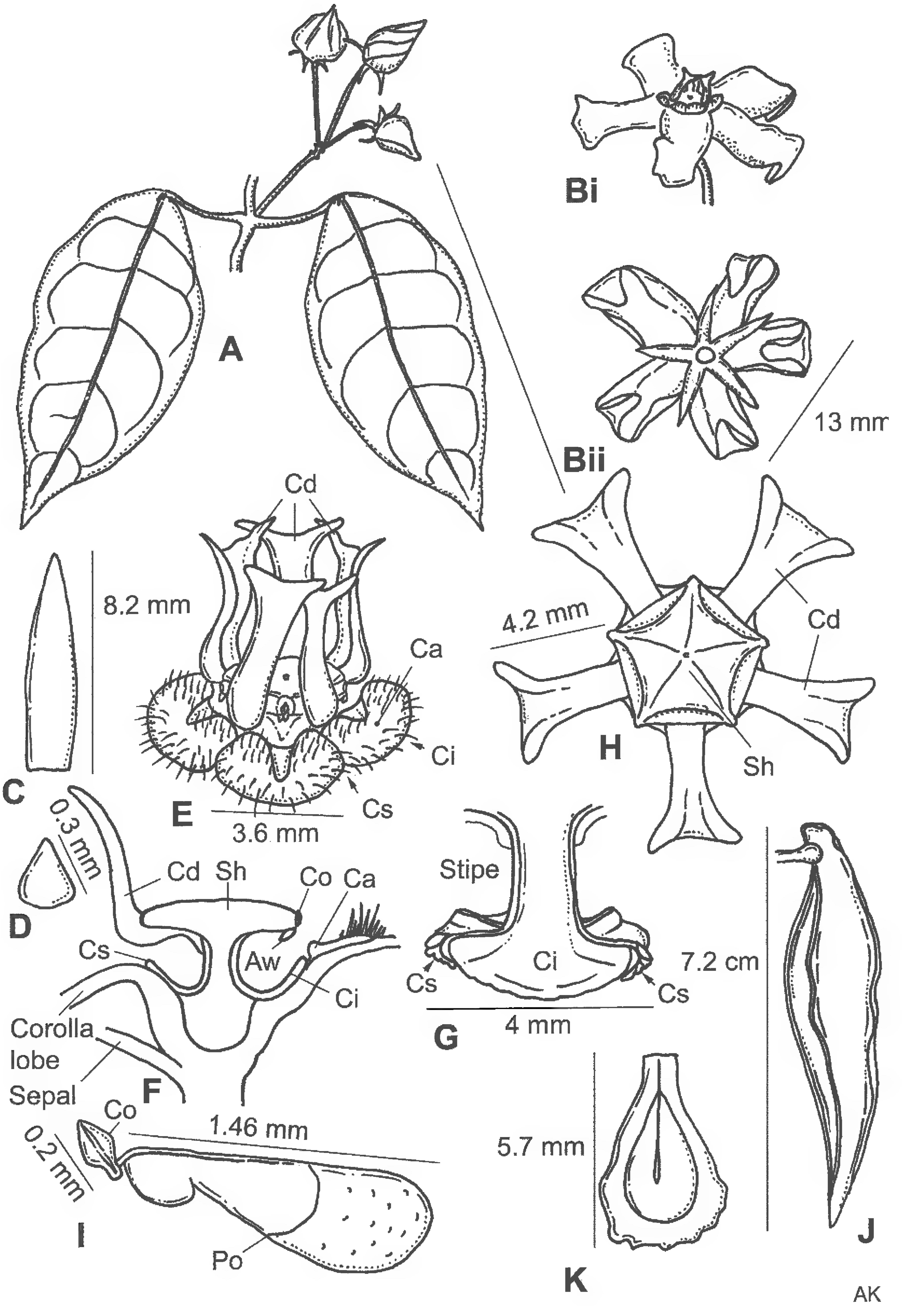

FIG. 9. *Gonolobus stapelioides*. **A.** Leaves and inflorescence. Bi. Open flower (adaxial view). Bii. Open flower (abaxial view). **C.** Sepal. **D.** Calycine colleter. **E.** Faucal annulus of the corolla, gynostegial corona, and style-head. **F.** Cross-section of flower. **G.** Detail of gynostegial corona of fused staminal (Cs) and interstaminal (Ci) segments and stipe (style-head removed). **H.** Style-head and laminar dorsal anther appendages (viewed from above). **I.** Pollinarium. **J.** Follicle. **K.** Seed. J–K based on *Bellingham 1487* (BM), rest based on *Krings 1394* (NCSC). **Aw** = anther wings; **Ca** = faucal annulus of corolla; **Ci** = interstaminal gynostegial corona segment; **Cd** = laminar dorsal anther appendage; **Co** = corpusculum; **Cs** = staminal gynostegial corona segment; **Po** = pollinium; **Sh** = style-head.

apices acute to narrowly obtuse, margins glabrous or very sparsely ciliolate, abaxial surface weakly and finely pubescent at the base and glabrous toward the apex, trichomes antrorsely-appressed, to 0.9 mm long; colleters 1 per sinus. Corolla lobes 5, oblong-ovate, 12–15 mm × 4–6.5 mm, slightly overlapping at the base, a glandular swelling frequently present in the sinus, margins and apices strongly recurved, adaxial surface papillate-pubescent along the right, abaxial surface essentially glabrous; faucal annulus (corolline corona or Ca) interrupted, a pronounced twin-peaked thickening opposite each corolla lobe, apparently reduced opposite each corolla lobe sinus, short-hispid; gynostegial corona of fused staminal (Cs) and interstaminal parts (Ci), single, erect-undulating, interstaminal secondary nectaries apparently absent or at least not formed into conspicuous bumps or mounds; anther guiderails without appendages, laminar dorsal anther appendages (Cd) white, ca. 4–4.2 × 1.8–2 mm, erect to spreading, apices bilobed; style-head 3.6–4.8 mm diam, stipe ca. 1.6 mm long, not toothed, though with white ribs present at the base of each anther. Pollinaria: corpuscula ca. 0.2 mm long, pollinia borne horizontally, ovate, ca. 1.5 mm × 0.41 mm. Follicles fusiform, 5-winged, 1.7 × 7.2 cm. Seeds pyriform, compressed, not plano-convex, 4.6–5.7 × 2.5–3.5 mm, glabrous, margins dentate, coma to 2.4 cm long.

Phenology.—Flowering January through June. Fruiting in June.

Distribution.—*Gonolobus stapelioides* is endemic to Jamaica. It is known only from montane rainforests from 1200–1660 m elevation.

Provisional conservation status.—IUCN: Least concern (LC). NatureServe: G4 N4.

Taxon concept mapping.— = *G. stapelioides* sensu Schlechter (1899); = *G. stapelioides* sensu Adams (1972).

Notes.—An appropriately labeled red type folder is present at P, but was found empty during visits in 2004 and 2006. In the absence of the specimen, *G. stapelioides* is neotypified here. Schlechter (1899) noted that Hamilton (loc. cit.) likely mixed up the localities when describing *G. stapelioides* and *G. virescens* Ham. The locality of the former was given as Tobago, and that of the latter as Jamaica. However, neither entity is known by any other specimen from the respective island indicated in the protologue. In addition, Hamilton's description of ovate and acute corolla lobes would be an inaccurate description of the Jamaican entity to which Schlechter (1899) and subsequent workers have applied the name *G. stapelioides*. However, Hamilton's corolla lobe description is a very nice match of the type of *G. virescens*. Thus, it appears that while the localities were mixed up, Hamilton's protologues clearly allow association of the name *G. stapelioides* to the Jamaican entity and *G. virescens* to the Tobagoan entity as Schlechter (1899) proposed.

Gonolobus stapelioides is immediately recognizable by the white Cd segments that are fully vertical at maturity (Fig. 9E, F).

Additional specimens examined. **JAMAICA. Portland Parish:** Vinegar Hill, 21 Feb 1894 (fl), *Harris 5561* (MO [a single leaf and a single flower]); Vinegar Hill, "6.2.95" [1895] (fl), *Harris 5561* (BM); Hardwar Gap, 25 Feb 1964 (fl), *Adams 12705* (M, MO); Immediately N of the Grand Ridge of the Blue Mountains, between John Crow Peak and Morce's Gap, 15 May 1989 (fl), *Bellingham 1156* (BM); 0.5 mi N of Hardwar Gap, near "The Waterfall," 14 Jan 1980 (fl), *Proctor 38534* (IJ); 0.5 mi N of Hardwar Gap, uphill from the trail above the "Waterfall," 3 Mar 2006 (fl), *Krings 1394 with Suiter and Proctor* (IJ, NCSC); 0.5 mi N of Hardwar Gap, uphill from the trail above the "Waterfall," 3 Mar 2006 (fl), *Krings 1396 with Suiter and Proctor* (IJ, NCSC). **St. Andrew Parish:** Grand Ridge of the Blue Mountains, E of the summit of John Crow Peak, 30 Apr 1990 (fl), *Bellingham 1211* (BM); Grand Ridge of the Blue Mountains, immediately E of John Crow Peak, 11 Jun 1991 (fl-sheet 1; fr-sheet 2), *Bellingham 1487* (BM-2 sheets). **St. Thomas Parish:** Monkey Hill, S spur of Mossmans Peak, 16 Jun 1952 (fl), *Proctor 6803* (BM, IJ).

7. Gonolobus stellatus Griseb., Fl. Brit. W.I. 420. 1862. (**Fig. 10**). TYPE: JAMAICA: Manchester, Knockpatrick, Nov 18[??] (fl), *Purdie s.n.* (HOLOTYPE: GOET!; ISOTYPES: BM!, K!).

Herbaceous perennial vines. Latex white. Stems pubescent to glabrate in age, both short, capitate-glandular, and longer, sharp, eglandular trichomes present, the latter retrorse-appressed or -spreading internodally, and antrorse-appressed along an indistinct, horizontal ridge between two opposing petioles and/or just above the node, to 1.25 mm long; nodes pubescent to glabrate, gland field apparently absent. Leaf blades elliptic to oblong-elliptic, 2.2–11.5 cm × 0.8–4.2 cm, apices acute or gradually acuminate with the acumen narrowly obtuse, to 1.4 cm long, bases cuneate, margins entire, adaxial surface sparsely strigose, abaxial

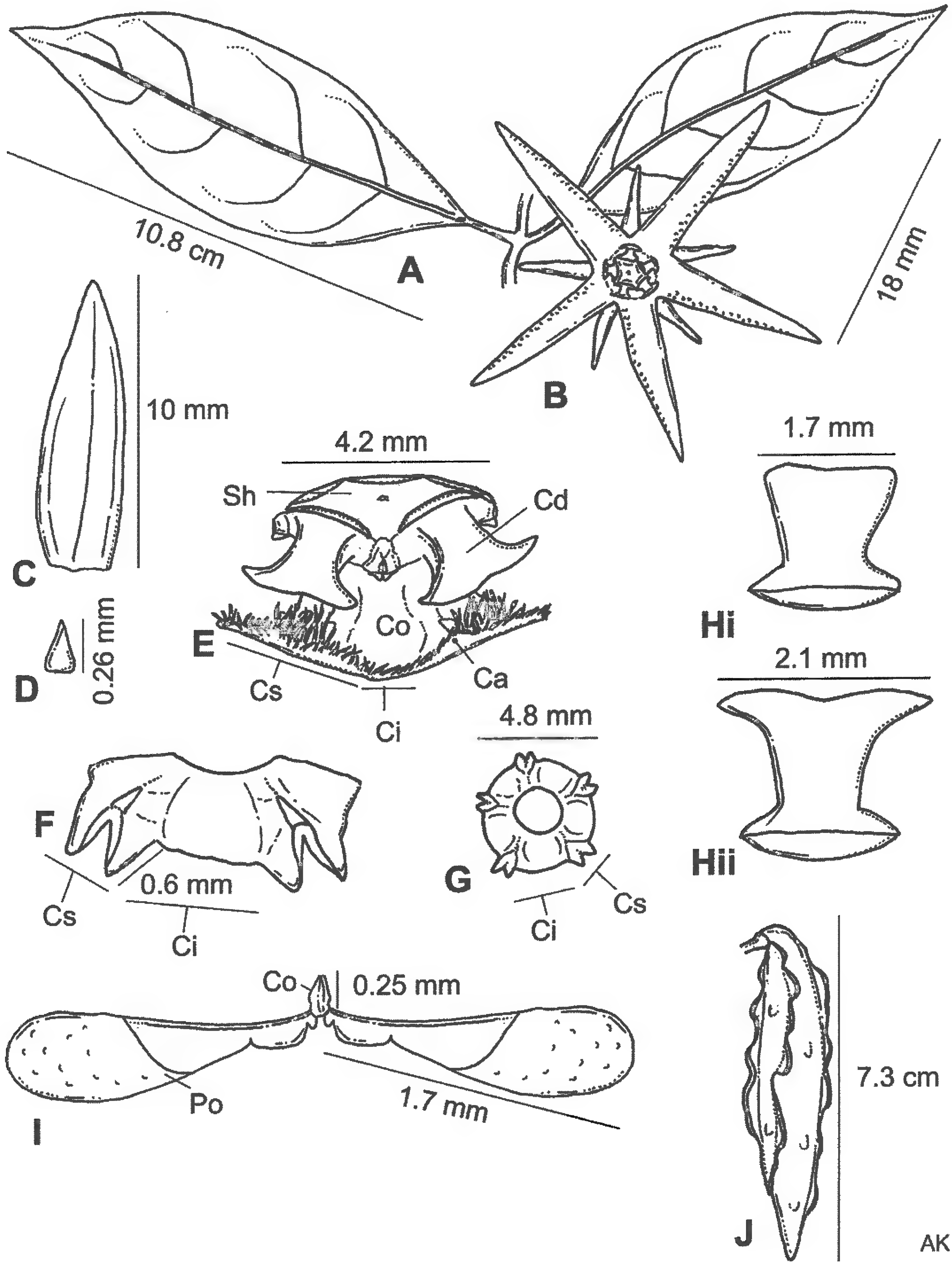

FIG. 10. *Gonolobus stellatus*. **A.** Leaves. **B.** Open flower. **C.** Sepal. **D.** Calycine colleter. **E.** Faucal annulus of the corolla, gynostegial corona, and style-head. **F.** Detail of gynostegial corona of fused staminal (Cs) and interstaminal (Ci) segments (side view). **G.** Detail of gynostegial corona (top view). Hi–ii. Variation in laminar dorsal anther appendages. **I.** Pollinarium. **J.** Follicle. A, C–D, and J based on *Proctor 29378* (BM). B and Hi–ii based on *Purdie s.n.* (K). E–G and I based on *Hunnewell 11032* (GH). **Aw** = anther wings; **Ca** = faucal annulus of corolla; **Ci** = interstaminal gynostegial corona segment; **Cd** = laminar dorsal anther appendage; **Co** = corpusculum; **Cs** = staminal gynostegial corona segment; **Po** = pollinium; **Sh** = style-head.

surface glabrate, trichomes sharp, eglandular, very sparsely scattered along the major and minor veins, colleters 2, 0.2–0.4 mm long; petioles 0.8–5.6 cm long, sparsely pubescent on all sides to glabrate, capitate-glandular trichomes, ca. 0.1 mm long, sharp, eglandular trichomes, ca. 0.6 mm long, antrorsely-appressed or -ascending; stipular colleters 2, ca. 0.25 mm long one borne on each side of the petiole base (rarely on the stem). Inflorescences racemiform, peduncles 0.7–3 cm long, sparsely pubescent to glabrate, capitate, as well as sharp, eglandular trichomes present, the latter antrorsely-appressed or -ascending, distributed throughout, ca. 0.8 mm long; pedicels 1.2–2.3 cm long, relatively evenly pubescent from apex to base, capitate-glandular trichomes ca 0.7 mm long, longer, sharp, eglandular trichomes antrorsely-ascending, ca. 0.26 mm long, bracts linear to linear-oblong, ca. 1.35 mm × 0.24 mm, caducous adaxial surface pubescence glabrous, abaxial surface coarsely pubescent, trichomes sharp, eglandular, ca. 0.22 mm long. Calyx lobes 5, lanceolate, 7–11 mm × 1.7–2.7 mm, apices obtuse, margins glabrous, abaxial surface very sparsely coarsely pubescent at the base, glabrous toward the apex, trichomes antrorsely appressed or -ascending, to 0.6 mm long; colleters 1–2 per sinus. Corolla lobes 5, linear-lanceolate, 15–18 mm × 4–5.3 mm, slightly lobed at the base, a glandular swelling frequently present in the sinus, adaxial surface densely strigillose, not papillate-pubescent, on the right half, abaxial surface glabrous; faucal annulus (corolline corona or Ca) interrupted, a raised bump or ridge opposite each corolla lobe sinus, pubescent; gynostegial corona of fused staminal (Cs) and interstaminal (Ci) parts, prostrate-undulating, single, secondary nectaries in interstaminal position absent; anther guiderails without appendages, laminar dorsal anther appendages (Cd) 1.7–2.1 mm wide, slightly emarginate to divergently and sharply bilobed; style-head ca. 4.3 mm diam, stipe ca. 1.7 mm long, edentate. Pollinaria: corpuscula ca. 0.25 mm long, pollinia borne horizontally, narrowly ovate, ca. 1.7 mm × 0.48 mm. Follicles (immature) fusiform, 5-winged, but with small murications between the wings, 7.1–7.3 cm × 1.6–1.7 cm. Seeds unknown.

Phenology.—Flowering in March and July. Fruiting in July.

Distribution.—Endemic to Jamaica, *G. stellatus* is known only from montane rainforests from about 390–460 m in elevation.

Provisional conservation status.—IUCN: Vulnerable (VU)—B1a,c. NatureServe: G3 N3.

Taxon concept mapping.— = *G. stellatus* sensu Schlechter (1899); = *G. stellatus* sensu Adams (1972).

Additional specimens examined. **JAMAICA. Portland Parish:** Hog House Hill study area, ca. 4 mi S of Sherwood Forest, N edge of John Crow Mtns., 1976–78 (st), *Kelly JCM 1490* (IJ); Gorge of Stony River above junction of the Macungo River, 25 Jul 1967 (fl & fr), *Proctor 29378* (BM, IJ). **St. Ann Parish:** County of Middlesex, Mt. Diablo, woods, 9 Mar 1936 (fl), *Hunnewell 11032* (GH).

8. Gonolobus stephanotrichus Griseb., Cat. Pl. Cub. 177. 1866. (**Fig. 11**). Type: CUBA: 1860–1864 (fl & fr), *Wright 2969* (Lectotype, designated by Krings & Fantz 2006: GOET!-fl; syntypes: BREM!, MO, G!, GH!, HAC!, K!, NY!, P!, UC!, US!).

Herbaceous perennial vines. Latex white (rarely watery). Stems pubescent, both short, capitate-glandular, and longer, sharp, eglandular trichomes present, the latter throughout, spreading, or retrorse internodally, and antrorse-appressed along an indistinct, horizontal ridge between two opposing petioles and/or just above the node, to 1.08 mm long; nodes pubescent, gland field apparently absent. Leaf blades lanceolate, ovate, or oblong-ovate, 2–14.4 cm × 0.7–7.7 cm, apices gradually or abruptly acuminate with the acumen narrowly obtuse, to 2 cm long, bases deeply cordate, margins entire, adaxial surface sparsely but evenly strigillose to glabrate, abaxial surface sparsely but evenly strigillose, sharp, eglandular trichomes scattered along the major and minor veins, to ca. 0.58 mm long, colleters 3–4, ca. 0.4 mm long; petioles 0.9–7 cm long, evenly pubescent on all sides, some trichomes capitate, to 0.1 mm long, but mostly sharp, eglandular, antrorsely ascending or spreading, to 0.67 mm long; stipular colleters 2, ca. 0. 39 mm long, one borne on each side of the petiole base (rarely on the stem). Inflorescences racemiform, peduncles 0.18–0.4 cm long, sparsely pubescent to glabrate, capitate trichomes apparently absent, sharp, eglandular trichomes sparse, antrorsely-appressed or -ascending, distributed throughout, ca. 0.4 mm long; pedicels 0.25–0.89 cm long, relatively evenly pubescent from apex to base, capitate-glandular trichomes very sparse, ca 0.07 mm long, longer, sharp, eglandular trichomes antrorsely-ascending, ca. 0.43 mm long, bracts linear-lanceolate, ca. 4.9 mm × 0.48 mm, caducous, adaxial surface glabrous, abaxial surface coarsely pubescent, trichomes sharp, eglandular,

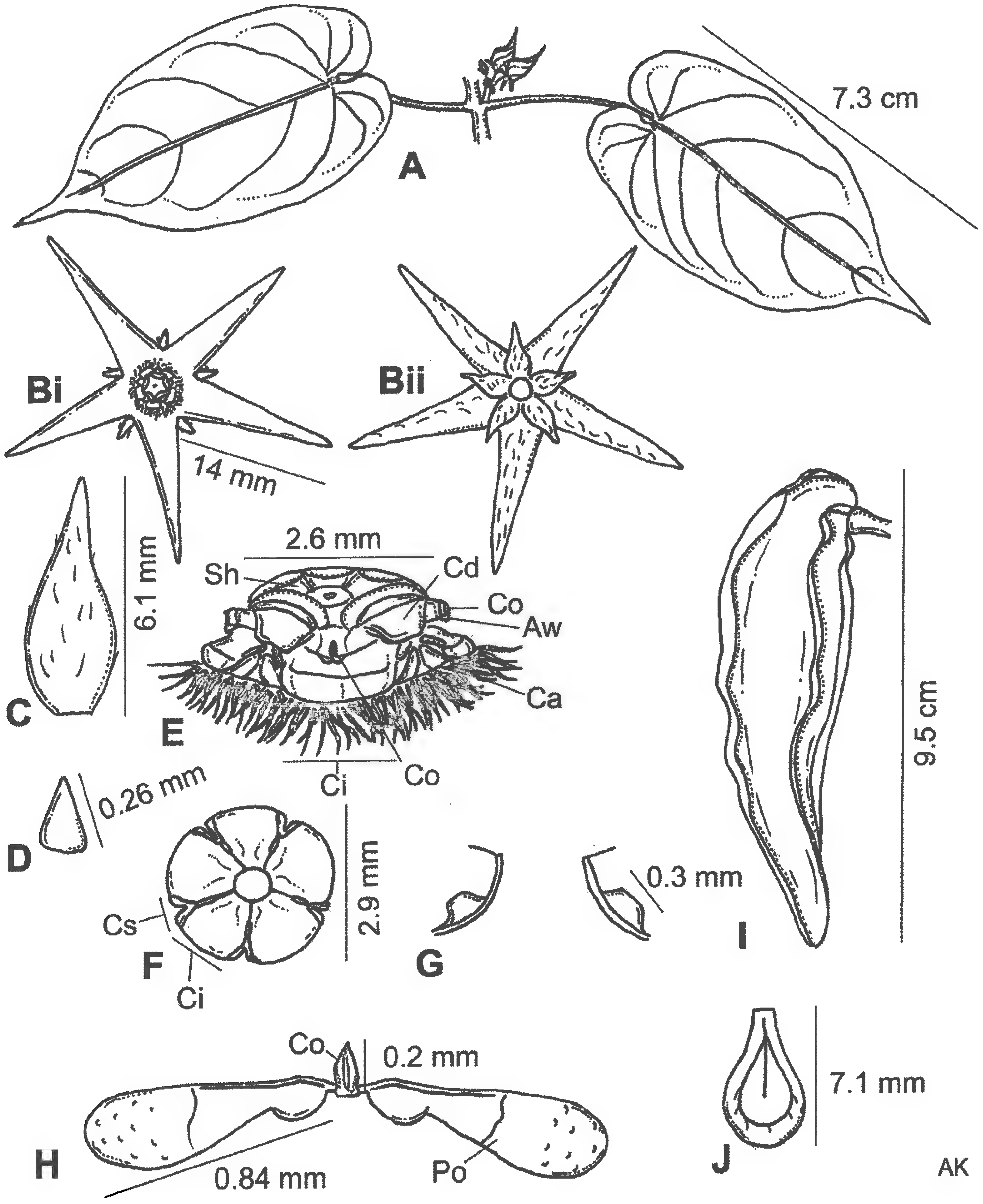

FIG. 11. *Gonolobus stephanotrichus*. **A.** Leaves and inflorescence. Bi. Open flower (adaxial view). Bii. Open flower (abaxial view). **C.** Sepal. **D.** Calycine colleter. **E.** Faucal annulus of the corolla, gynostegial corona, and style-head. **F.** Detail of gynostegial corona of fused staminal (Cs) and interstaminal (Ci) segments (top view). **G.** Detail of gynostegial stipe and basal tooth. **H.** Pollinarium. **I.** Follicle. **J.** Seed. A–D based on *Wright 2969* (NY). E–H based on *Acevedo-Rodríguez 10596* (US). I–J based on *Acevedo-Rodríguez 11445* (US). **Aw** = anther wings; **Ca** = faucal annulus of corolla; **Ci** = interstaminal gynostegial corona segment; **Cd** = laminar dorsal anther appendage; **Co** = corpusculum; **Cs** = staminal gynostegial corona segment; **Po** = pollinium; **Sh** = style-head.

0.22–0.47 mm long, antrorse. Calyx lobes 5, lanceolate, 2.7–6.7 mm × 1.6–2 mm, apices obtuse, margins glabrous, abaxial surface sparsely but coarsely pubescent, trichomes antrorsely appressed or -ascending, to 0.4 mm long; colleters 1 per sinus. Corolla lobes 5, elongate triangular or lanceolate, 8.7–14 mm × 2.4–3.7 mm, slightly lobed at the base, a glandular swelling frequently present in the sinus, adaxial surface glabrous, abaxial surface pubescent with coarse, sharp, eglandular, antrorsely-appressed or -ascending trichomes, ca. 0.7 mm long; faucal annulus (corolline corona or Ca) annular, pubescent; gynostegial corona of fused staminal (Cs) and interstaminal (Ci) parts, prostrate-undulating, single, secondary nectaries in interstaminal position absent or at least not developed into distinct bumps or mounds; anther guiderails without appendages, laminar dorsal anther appendages (Cd) ca. 0.6 mm wide, truncate; style-head ca. 2.6 mm diam, stipe ca. 0.73 mm long, teeth not appearing as notches, instead truncate, borne individually on the lower portion of the column, just above the upwardly rising segment of each Cs. Pollinaria: corpuscula ca. 0.2 mm long, pollinia borne horizontally, narrowly ovate, ca. 0.84 mm × 0.3 mm. Follicles ovoid, 5-winged, 9.3–9.5 mm × 2.6–2.9 mm. Seeds pyriform, compressed, not plano-convex, 7–7.8 mm × 3.4–4.9 mm, glabrous, margins entire, not dentate, coma to 2.7 cm long.

Phenology.—Flowering in January, February, May, June, and October. Fruiting in April, November, and September.

Distribution.—*Gonolobus stephanotrichus* occurs in Cuba, Hispaniola, and Puerto Rico (Fig. 1). It has primarily been collected in mid-elevation (340–1100 m), moist to wet forests.

Provisional conservation status.—IUCN: Least concern (LC). NatureServe: Cuba (G4 N4); Dominican Republic (G4 N4); Puerto Rico (G4 N4).

Taxon concept mapping.— = *G. stephanotrichus* sensu Schlechter (1899); = *G. stephanotrichus* sensu Liogier (1957, 1994, 1995); = *G. stephanotrichus* sensu Acevedo-Rodríguez (2005).

Notes.—*Gonolobus stephanotrichus* was recently "re-discovered" from Cuba, from where it had been known only by collections sometime between 1860 and 1864 (Krings et al. 2005). Additional illustrations of *G. stephanotrichus* from Puerto Rico can be found in Acevedo-Rodríguez (2005). Readers should note however, that the gynostegium pictured in fig. 36 D should be rotated so that the Cd are opposite the corolla lobe sinuses and not opposite the corolla lobes themselves as pictured.

Additional specimens examined. **CUBA:** Cuba Orientali, 1856–1857 (fl, fr-imm), *Wright 407* (GH; blue label); Cuba Orientali, 1861 [1860 on white label, but with a one marked through the zero] (fl, fr-imm), *Wright 164* (S). **Santiago de Cuba:** Sierra Maestra, Parque Nacional Turquino, within 3 km of Campamento Joaquín on trail from the Alto de Naranjo, 3 June 2005 (fl-imm), *Krings, Areces, and Lazcano s.n.* (HAJB, NCSC); Sierra Maestra, Parque Nacional Turquino, 2–3 km downhill from Campamento Joaquín in direction of the Alto de Naranjo, 2 June 2005 (fl-imm), *Krings, Areces, and Lazcano s.n.* (NCSC). **DOMINICAN REPUBLIC. Espaillat:** Cordillera Septentrional, Mora, Colonia de Jamao, 21 May 1929 (fl), *Ekman H12568* (K). **Puerto Plata:** estribo sur de Isabel de Torres, 16 Oct 1976 (fl), *Liogier and Liogier 25627* (JBSD). **San Cristóbal:** Cordillera Central, Loma La Humeadora, ladera este, en el nacimiento del Arroyo Derrumdadero, 20 Apr 1994 (fr), *Jiménez, Mejía, and Veloz 1304* (JBSD). **PUERTO RICO. Adjuntas:** Barrio Guilarte, Guilarte Forest Reserve, along trail, 21 Nov 1997 (fr), *Romero and Nazario s.n.* (UPRRP). **Arecibo:** Río Abajo State Forest Reserve, 18 Jan 1996 (st), *Acevedo-Rodríguez and Axelrod 7785* (US); Río Abajo State Forest, along Igartua trail, 12 Jan 1999 (fl), *Acevedo-Rodríguez 10596* (UPRRP, US); Río Abajo State Forest, 2 Feb 1999 (fl), *Acevedo-Rodríguez 10814* (UPRRP, US); Río Abajo State Forest, along Igartua trail, 20 Apr 2006 (st), *Krings 1390* (NCSC); Río Abajo State Forest, 20 Apr 2006 (st), *Krings 1391* (NCSC); Río Abajo State Forest, 20 Apr 2006 (st), *Krings 1392* (NCSC). **Orocovis:** Toro Negro Forest Recreation area, 11 Sep 2000 (fr), *Acevedo-Rodríguez 11445* (UPRRP, US); Toro Negro State Forest, near uphill end of Sendero Piscina where it joins with Camino del Bolo, 21 Apr 2006 (st), *Krings 1387* (NCSC); Toro Negro State Forest, Sendero Piscina, trailside, 21 Apr 2006 (st), *Krings 1388* (NCSC); Toro Negro State Forest, trail beside Quebrada Doña Juana on opposite side of river from Rt 143 entrance to camping area, 21 Apr 2006 (st), *Krings 1389* (NCSC).

9. Gonolobus waitukubuliensis Krings, Syst. Bot. 32:187. 2007. (**Fig. 12**). Type: DOMINICA: In sylvis ad Laudat, May 1882 (fl), *Eggers 728* (holotype: HBG!; isotypes: FR!, G!, GH!, JE!, M!, P!, W!, Z!).

Herbaceous perennial vines. Latex white. Stems glabrous or glabrate, both short, capitate-glandular, and longer, sharp, eglandular trichomes present, the latter mostly retrorse or spreading internodally, and antrorse-appressed along an indistinct, horizontal ridge between two opposing petioles and/or just above the node, to 0.64 mm long; nodes pubescent or glabrous in age, gland field sometimes present. Leaf blades ovate to oblong-ovate, (2.1–)6.7–10.4 cm × (0.9–)3.2–5.7 cm, apices gradually or abruptly acuminate with the acumen

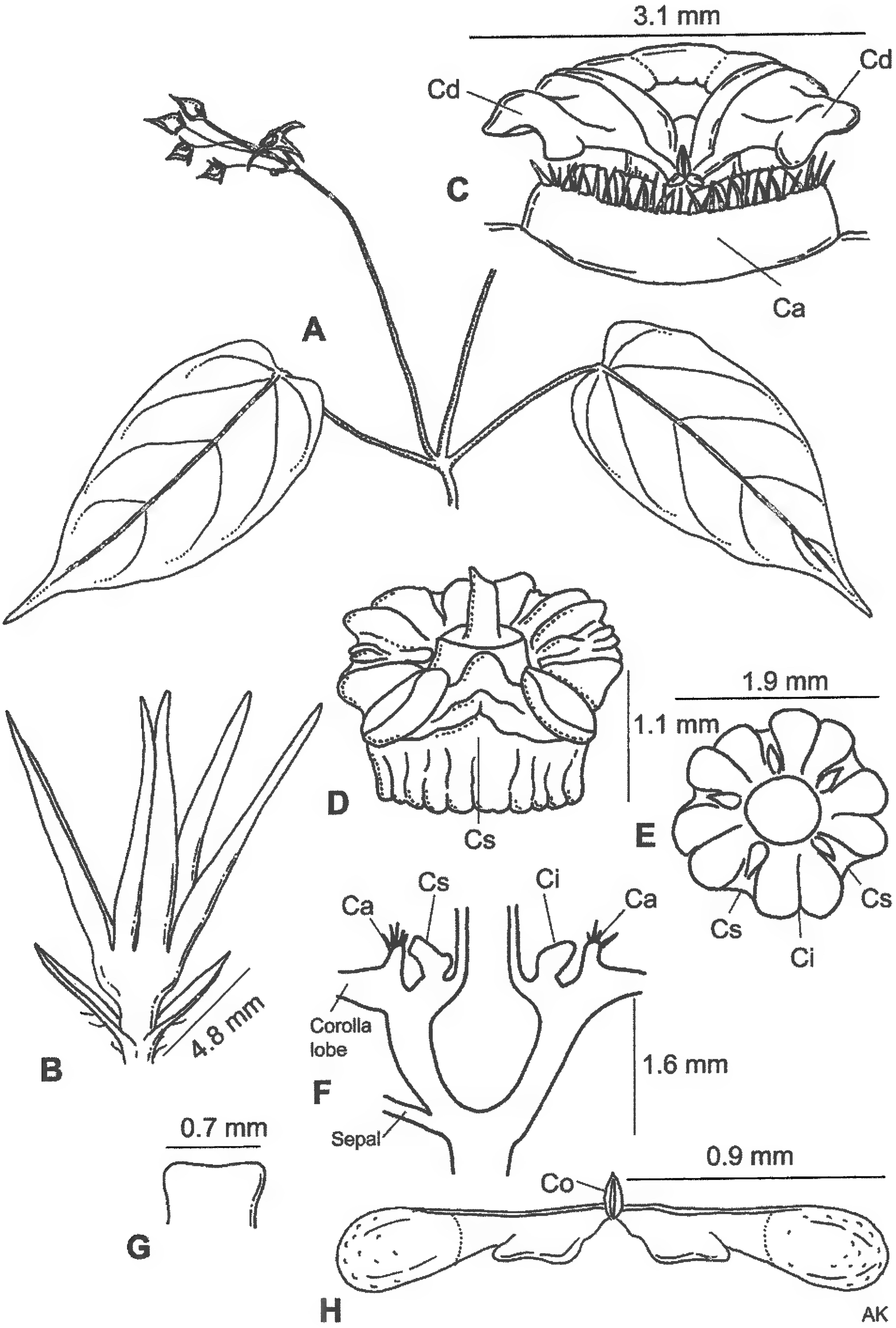

FIG. 12. *Gonolobus waitukubuliensis*. **A.** Leaves and inflorescence. **B.** Flower. **C.** Raised and completely circular faucal annulus of the corolla (Ca) and style-head (gynostegial corona obscured behind the Ca). **D.** Gynostegial corona of fused staminal (Cs) and interstaminal (Ci) segments (style-head removed). **E.** Top view of gynostegial corona (style-head removed). **F.** Cross-section of corolla tube showing position of corollar and gynostegial corona elements. **G.** Laminar dorsal anther appendage (Cd). **H.** Pollinarium. A and C based on *Eggers 728* (M). B and D–H based on *Webster 13505* (US). **Ca** = faucal annulus of corolla; **Ci** = interstaminal gynostegial corona segment; **Cd** = laminar dorsal anther appendage; **Co** = corpusculum; **Cs** = staminal gynostegial corona segment.

acute, to 1.8 cm long, bases deeply or shallowly cordate (rarely rounded, but then other leaves present with cordate bases), margins entire, adaxial surface glabrate or sparsely strigose, abaxial surface glabrate or more densely strigose with sharp, eglandular trichomes scattered along the major and minor veins, colleters 2, (0.4–)0.7–0.9 mm long; petioles (0.9–)2.2–5.4 cm long, glabrate or sparsely pubescent primarily along the adaxial side and near the apex on the abaxial side, trichomes mostly capitate, to 0.09 mm long, with some short, sharp, eglandular trichomes mixed in, 0.2–0.4 mm long; stipular colleters 2, ca. 0.3 mm long, one borne on each side of the petiole base. Inflorescences racemiform, peduncles 4.1–5.2 cm long, glabrous or very sparsely pubescent with both capitate and sharp, eglandular hairs present, the latter antrorsely-appressed or –ascending, most pronounced near apex, ca. 0.3 mm long; pedicels 1.4–3.4 cm long, pubescence pronounced at apex and essentially absent elsewhere or sparsely to densely, relatively evenly pubescent from apex to base, capitate-glandular trichomes ca. 0.08 mm long, longer, sharp, eglandular hairs antrorsely- appressed or -ascending, ca. 0.3 mm long, bracts linear-lanceolate, ca. 0.8 mm × 0.2 mm, caducous, adaxial surface glabrous, abaxial surface coarsely pubescent, trichomes sharp, eglandular, ca. 0.17 mm long, antrorse. Calyx lobes 5, sublanceolate to elongate triangular (widest at or just above the base), 2.2–5.3 mm × 0.8–1.4 mm, apices obtuse to narrowly rounded, margins glabrous, abaxial surface glabrous or pubescent primarily at the base and variously toward the apex, trichomes, if present, antrorsely-ascending or -appressed, to 0.27 mm long; colleters 1 per sinus. Corolla lobes 5, narrowly lanceolate to elongate triangular, 4.2–11.2 mm × 1.8–3.4(–3.7) mm, slightly lobed at the base, a glandular swelling frequently present in the sinus, adaxial surface glabrous, abaxial surface glabrous; faucal annulus (corolline corona or Ca) a distinctly raised ring, ca. 0.5 mm high, short-hispid along the entire rim or only opposite each corolla lobe sinus; gynostegial corona of fused staminal (Cs) and interstaminal (Ci) parts, single, fused at the base into an erect ring, 5-lobed, lobes appearing strongly folded; anther guiderails apparently without appendages, laminar dorsal anther appendages (Cd) 0.6–0.9 mm wide, emarginate or truncate; style-head 2.8–3.14 mm diam, stipe 1–1.5 mm long, not toothed. Pollinaria: corpuscula 0.14–2 mm long, pollinia borne horizontally, ovate, ca. 0.6–0.85 mm × 0.3–0.38 mm. Follicles unknown.

Phenology.—Flowering in March, May, June, and July.

Distribution.—*Gonolobus waitukubuliensis* is endemic to Dominica (Fig. 1). It has been found primarily in middle elevation rainforests (ca. 609–1067 m; 2000–3500 ft). Like most West Indian *Gonolobus* taxa, *G. waitukubuliensis* appears to require small gaps in mature forests. It does not appear to be able to compete in large gaps or roadside edges in which other vines quickly become dominant. It is rather infrequent to rare, especially in mature forests with few gaps.

Provisional conservation status.—IUCN: Vulnerable (VU)—B1a,c. NatureServe: G3 N3.

Taxon concept mapping.— < *G. martinicensis* sensu Schlechter (1899); < *G. martinicensis* sensu Howard (1988); < *G. martinicensis* sensu Nicolson (1991).

Notes.—*Gonolobus waitukubuliensis* is immediately recognizable among Lesser Antillean *Gonolobus* species by the combination of a distinctly raised, completely circular faucal annulus (ca. 0.5 mm tall), an erect gynostegial corona that appears quite folded apically, and a relatively tall gynostegial stipe (1–1.5 mm). It shares with *G. absalonensis*, *G. iyanolensis*, and sometimes *G. martinicensis*, the absence of hairs from the abaxial corolla lobe surface. The trichomes of the pedicel are fine and not as long (ca. 0.3 mm) as in *G. iyanolensis* (0.3–0.9 mm).

Additional specimens examined. **DOMINICA:** Mar 1882 (fl), *Eggers s.n.* (US); July 1882 (fl), *Eggers 1100* (K); May 1882 (fl), *Eggers 1700* (MO); s.d. (fl), *Imray 263* (K); St. John/St. Peter, Hiking trail to Morne Diablotins, 3 May 2006 (st), *Krings 1375, 1376, 1377* (NCSC); St. John/St. Peter, Syndicate hiking trail, 3 May 2006 (st), *Krings 1378* (NCSC); St. John/St. Peter, Hiking trail to Morne Diablotins, 4 May 2006 (st), *Krings 1380* (NCSC); St. John/St. Peter, Hiking trail to Morne Diablotins, 4 May 2006 (st), *Krings 1381* (NCSC); St. John/St. Peter, Hiking trail to Morne Diablotins, 4 May 2006 (st), *Krings 1382, 1383, 1384* (NCSC); St. John/St. Peter, Hiking trail to Morne Diablotins, at opening in trail with westward vista of Portsmouth and Cabrits, 4 May 2006 (st), *Krings 1385* (NCSC); St. John/St. Peter, Hiking trail to Morne Diablotins, 4 May 2006 (st), *Krings 1386* (NCSC); St. Joseph, En Haut Jean, 24 Jun 1965 (fl), *Webster 13505* (BM, US).

10. Gonolobus youroumaynensis Krings, Syst. Bot. 32:191. 2007. (**Fig. 13**). Type: ST. VINCENT: Orange Hill Estate, roadbank in banana and pigeon pea plantations, uphill from fork in road to the Central Water and Sewage Authority water intake site, Kiss-me, 14 Mar 2006 (fl), *Krings 1374 with Springer* (holotype: NCSC!; isotypes: GH!, K!, NY!, US!, P!).

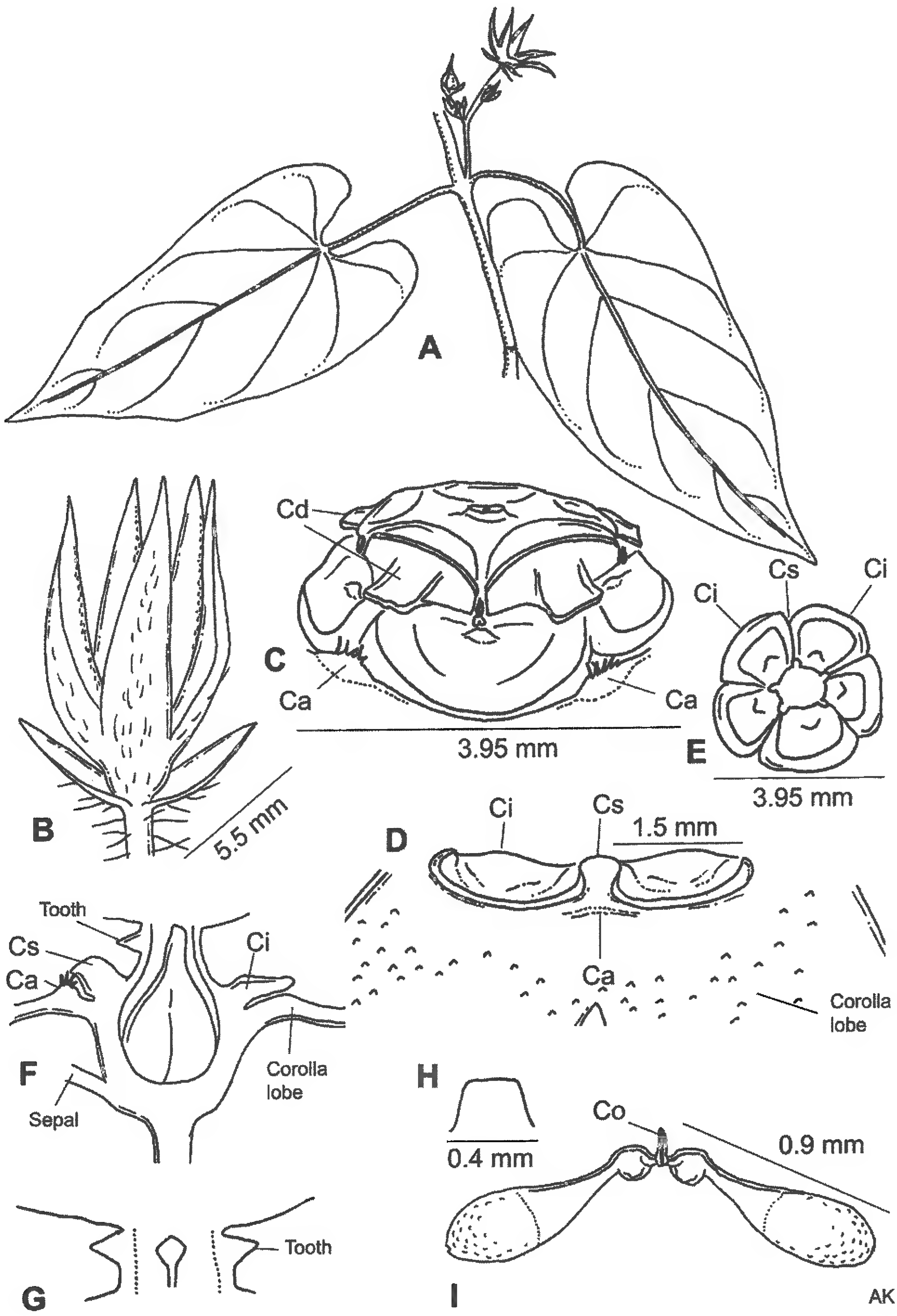

FIG. 13. *Gonolobus youroumaynensis*. **A.** Leaves and inflorescence. **B.** Flower showing coarse abaxial corolla lobe pubescence. **C.** Faucal annulus of the corolla (Ca), gynostegial corona, and style-head. **D.** Gynostegial corona of fused staminal (Cs) and interstaminal segments (Ci) (style-head removed). **E.** Top view of gynostegial corona (style-head removed). **F.** Cross-section of corolla tube showing position of corollar and gynostegial corona elements. **G.** Detail of teeth of the gynostegial stipe. **H.** Laminar dorsal anther appendage (Cd). **I.** Pollinarium. A–B and D based on *Howard 19584* (GH, NY, US). C and E–I based on *Krings 1374 with Springer* (NCSC). Ca = faucal annulus of corolla; Ci = interstaminal gynostegial corona segment; Cd = laminar dorsal anther appendage; Co = corpusculum; Cs = staminal gynostegial corona segment.

Herbaceous perennial vines. Latex white. Stems glabrate to pubescent, both short, capitate-glandular, and longer, sharp, eglandular trichomes present, the latter throughout, spreading, or retrorse internodally, and antrorse-appressed along an indistinct, horizontal ridge between two opposing petioles and/or just above the node, to 1.2 mm long; nodes pubescent, gland field apparently absent. Leaf blades ovate to oblong-ovate, (3.0–)5.4–9.6 cm × (1.2–)2.4–6.3 cm, apices gradually or abruptly acuminate with the acumen narrowly obtuse, to 1.5 cm long, bases deeply or shallowly cordate, margins entire, adaxial surface glabrate or sparsely strigose, abaxial surface glabrate or more densely strigose with sharp, eglandular trichomes scattered along the major and minor veins, colleters 2–4, 0.35–1 mm long; petioles (1.2–)2.7–5.3 cm long, spreading pubescent on all sides, some trichomes capitate, to 0.09 mm long, but mostly sharp, eglandular, 1–1.2 mm long; stipular colleters 2, ca. 0.26 mm long, one borne on each side of the petiole base. Inflorescences racemiform, peduncles 0.7–3.1 cm long, capitate, as well as sharp, eglandular trichomes present, the latter mostly spreading, but also some antrorsely-appressed or -ascending, distributed throughout, 0.7–0.9 mm long; pedicels 1.3–1.8 cm long, relatively evenly pubescent from apex to base, capitate-glandular trichomes ca 0.08 mm long, longer, sharp, eglandular trichomes mostly spreading, but some antrorsely-appressed or -ascending, ca. 0.9 mm long, bracts linear-lanceolate, 1.1–1.7 mm × 0.2–0.25 mm, caducous, adaxial surface glabrous, abaxial surface coarsely pubescent, trichomes sharp, eglandular, ca. 0.53 mm long, antrorse. Calyx lobes 5, sublanceolate to elongate triangular (widest at or just above the base), 3.8–5.8 mm × 1–1.3 mm, apices obtuse to narrowly rounded, margins ciliate or glabrate, abaxial surface densely and coarsely pubescent at the base and variously toward the apex, trichomes spreading and antrorsely appressed or -ascending, to 0.8 mm long; colleters 1 per sinus. Corolla lobes 5, narrowly lanceolate to elongate triangular, (7.5–)8.7–10.1 mm × 1.9–3.1 mm, slightly lobed at the base, a glandular swelling frequently present in the sinus, adaxial surface pubescent on the right half, trichomes capitate, ca. 0.1 mm long, abaxial surface pubescent with coarse, sharp, eglandular, antrorsely-appressed or -ascending trichomes, particularly at the base and variously toward the apex, 0.36–0.5 mm long; faucal annulus (corolline corona or Ca) interrupted, a raised bump or indistinct ridge opposite each corolla lobe sinus, pubescent or glabrous; gynostegial corona of fused staminal (Cs) and interstaminal (Ci) parts, prostrate-undulating, single, a small bump borne near the base in the interstaminal position; anther guiderails without appendages, laminar dorsal anther appendages (Cd) ca. 0.5 mm wide, rounded or truncate; style-head 2.8–3.95 mm diam, stipe 0.48–0.7 mm long, bearing a single tooth ca. 0.2 mm long below each anther. Pollinaria: corpuscula 0.2–0.23 mm long, pollinia borne horizontally, ovate, 0.6–0.9 mm × 0.32–0.45 mm. Follicles unknown.

Phenology.—Flowering in February and March.

Distribution.—*Gonolobus youroumaynensis* is apparently endemic to St. Vincent (Fig. 1). It occurs on the windward side of the island at the foot of La Soufrière in the Orange Hill Estate area. Vines were found growing along the road to the water intake amidst banana and pigeon pea plantations. Vines were not found along the trail to the crater of La Soufrière. However, only a half day was spent searching this trail and they could have been overlooked.

Provisional conservation status.—IUCN: Critically Endangered (CR)—B1a,biii. NatureServe: G1 N1.

Taxon concept mapping.— < *G. martinicensis* sensu Schlechter (1899); < *G. martinicensis* sensu Howard (1988).

Notes.—*Gonolobus youroumaynensis* is readily recognizable among Lesser Antillean *Gonolobus* species by the combination of a single, prostrate-undulating gynostegial corona exhibiting a small bump towards the base of the Ci, a toothed stipe, and long, spreading trichomes (to 0.9 mm) found on stems, peduncles, and pedicels.

Additional specimens examined. **ST. VINCENT:** Mar 1890 (fl), *Smith and Smith 382* (BM, E, GH, K, NY); Orange Hill Estate, 10 Feb 1980 (fl), *Howard 19584* (BM, GH, NY, US).

DOUBTFUL AND EXCLUDED NAMES

The following list includes names that are excluded from *Gonolobus* s.s. based on their morphology (e.g.,

lack of laminar dorsal anther appendages), and names of uncertain status. Two new combinations are made below: *Matelea dictyopetala* and *M. pubescens*.

Gonolobus bakeri Schltr., Symb. antill. 7(3):341. 1912. TYPE: CUBA: Cult. in Santiago de las Vegas, May 1907, *Baker 7286* (HOLOTYPE: location unknown).

Gonolobus bakeri is apparently only known from the type collection, which has not been located despite query of nearly one hundred institutions known to house West Indian collections. If the specimen was at B, it may have been destroyed in WW II. The position of *G. bakeri* appears uncertain. Schlechter does not describe dorsal anther appendages in the protologue. Combined with his note that the species is "mit *G. variifolius* Schltr. [now *Matelea variifolia* (Schltr.) Woodson] am nächsten verwandt," there is reason to believe that *G. bakeri* may better belong in *Matelea*. *Matelea variifolia* clearly lacks laminar dorsal anther appendages and also exhibits suborbicular corolla lobes. It is known only from Puerto Rico (Schlechter 1899; Acevedo-Rodríguez 2003, 2005). As the single specimen representing *G. bakeri* was cultivated in Cuba, it may be that the species is merely a pubescent form of *M. variifolia*. Among West Indian *Gonolobus* s.s. (if not the entire genus), *G. bakeri* would be the only species with suborbicular corolla lobes.

Gonolobus bayatensis Urb., Symb. antill. 9(3):420. 1925. TYPE: CUBA: Oriente, Bayate, 9 Oct 1914, *Engström 3056* (LECTOTYPE, designated by Krings 2008: S!; ISOLECTOTYPE: NY!) ≡ *Matelea bayatensis* (Urb.) Woodson, Ann. Missouri Bot. Gard. 28:226. 1941.

Gonolobus bicolor (Britton & P.Wilson) Urb., Symb. antill. 9(3):421. 1925. TYPE: CUBA: Oriente, Maestra ridge, 1300 m, Jul 1922, *León 10787* (HOLOTYPE: NY!) ≡ *Matelea bicolor* (Britton & P. Wilson) Woodson, Ann. Missouri Bot. Gard. 28:236. 1941.

Gonolobus dictyopetalus Urb. & Ekman, Ark. Bot. 20A(5):41. 1926. TYPE: HAITI: Massif de la Selle, Morne Cabaio, c. 1900 m, 24 Aug 1924 (fl), *Ekman H1625* (LECTOTYPE: S!, designated by Krings 2008; ISOLECTOTYPE: IJ! – fragment [single leaf]) ≡ *Matelea dictyopetala* (Urb. & Ekman) Krings, **comb. nov.**

Gonolobus domingensis Alain, Moscosoa 1(3):46. 1978. TYPE: DOMINICAN REPUBLIC: Estribo sur del Isabel de Torres, Puerto Plata, alt. 750 m, 16–17 Aug 1975 (fl), *Liogier & Liogier 23780* (LECTOTYPE: JBSD!, designated by Krings 2005d) ≡ *Matelea domingensis* (Alain) Krings, Sida 21:2081. 2005.

Gonolobus floccosus Bertol., Opusc. Sci. 4:225. 1823. TYPE: GUADELOUPE: (HOLOTYPE: BOLO!) = *Matelea maritima* (Jacq.) Woodson, Ann. Missouri Bot. Gard. 28:222. 1941.

Gonolobus grisebachianus Schltr. in Urb., Symb. antill. 1(2):287. 1899. TYPE: CUBA: *Wright s.n.* (HOLOTYPE: location unknown) ≡ *Matelea grisebachiana* (Schltr.) Alain, Mem. Soc. Cub. Hist. Nat. "Felipe Poey" 22:120. 1955.

Matelea grisebachiana is apparently known only from the type collection, which has not been located despite query of nearly one hundred institutions known to house West Indian collections. If it was at B, it may have been destroyed in WW II. Thus, the species can be placed solely based on the protologue and past treatments. Although Krings et al. (2005) maintained the taxon in *Gonolobus*, the combination in *Matelea* may be more correct based on the glabrous, reticulate corolla lobes and very narrow, linear-lanceolate leaves (0.5-0.7 cm wide)—a leaf form quite atypical for *Gonolobus*. The description of the corolla lobes as being 9 cm long, is likely a print-setting error to be corrected to 9 mm. Grisebach (1866) did not mention laminar dorsal anther appendages in his protologue for *G. tigrinus* var. *angustifolia* and, upon reconsideration, it is unclear to me whether Schlechter (1899) was refering to them or not [italics mine]: "Diese Art ist trotz ihrer habituellen Aehnlichkeit mit *G. tigrinus* Griseb. von diesem vollständing verschieden. Die Blätter sind schmaler, die Blüthen grösser, die äussere Corona ganz verschieden und die *Schuppen der inneren Corona viel deutlicher vom Antherenrücken abgehoben*, ausserdem, von oben gesehen, in der Mitte nicht ausgerandet, sondern eher verdickt." I am hesitant to presume the taxon extinct, as another Cuban Gonolobinae species—*G. stephanotrichus*—was recently rediscovered in the country after having been known from the island only from the type, collected between 1860 and 1864 (Krings et al. 2005).

Gonolobus haitiensis P.T. Li, J. South China Agric. Univ. 14:58. 1993. TYPE: HAITI: Massif du Nord, St. Louis du Nord, Morne Baron, 950 m, 20 Aug 1925, *Ekman H4693* (HOLOTYPE: S!; ISOTYPES: B!, US!). = *Matelea crispiflora* (Urb.) Jiménez, Rhodora 62:238. 1960, syn. nov.

Gonolobus haitiensis P.T. Li is a nomen novum for *Gonolobus stipitatus* Alain (Phytologia 64:345. 1988). It is here reduced to synonymy beneath *Matelea crispiflora*, as its type (*Ekman H4693*) clearly belongs with *Poicillopsis crispiflora* Urb. However, see also note for *Gonolobus membranaceus* Schltr.

Gonolobus maritimus (Jacq.) R.Br., Mem. Wern. Nat. Hist. Soc. 1:24. 1810. Type: Herbar. Du Jacquin, 2 Insulae Caribaea, s.d., De Ponthieu (lectotype, designated by Krings & Saville 2007: BM!) ≡ *Matelea maritima* (Jacq.) Woodson, Ann. Missouri Bot. Gard. 28:222. 1941.

Gonolobus membranaceus Schltr. in Urb., Symb. antill. 1(2):285. 1899. Type: HAITI: *Poiteau s.n.* (holotype: location unknown) = *Matelea crispiflora* (Urb.) Jiménez, Rhodora 62:238. 1960.

The location of the type remains unknown. *Ekman H4693* (IJ!) is labelled *Gonolobus membranaceus*. The specimen consists of mostly stem and 3–4 leaf fragments held in a fragment pocket. It appears to match *Poicillopsis crispiflora* Urb. *Gonolobus membranaceus* is likely very closely related to *Matelea haitiensis* as, based on the protologues, the two appear to differ only in the shape and apices of the leaf blades and calyx lobes. Additional collections and discovery of the type may prove them synonymous.

Gonolobus nipensis Urb., Symb. antill. 9(3):421. 1925. Type: CUBA: Oriente, Sierra de Nipe, Loma Mensura, c. 725 m, 11 Jul 1919 (fr), *Ekman 9710* (lectotype, designated by Krings 2008: S!; isolectotype: NY!). ≡ *Matelea nipensis* (Urb.) Woodson, Ann. Missouri Bot. Gard. 28:226. 1941.

Gonolobus ottonis C. Koch & Bouche, Ind. Sem. Hort. Berol. 13. 1855. Type: unknown.

Sometimes cited as *Gonolobus ottonis* Walp. (Ann. Bot. Syst. 5:502. 1859.). However, Walpers (1859) clearly cited *G. ottonis* C. Koch & Bouche and should not be considered author of a homonym. Walpers (1859) repeated Koch and Bouche's citation: 'Ex insula Cuba reportavit *Otto*.' However, Schlechter (1899) thought that the specimen collected by Otto (apparently formerly at B) was from Caracas, Venezuela, not from Cuba. The location of the type is unknown.

Gonolobus oxyanthus Turcz., Bull. Soc. Imp. Naturalistes Moscou 25(2):318. 1852. Type: VENEZUELA: 1845–1852, *Funk 2* (G, n. v.; P, n. v.) fide TROPICOS.

Fide Fontella and Schwarz (1981), a synonym of *Gonolobus rostratus* (Vahl) R. Br. ex Schult. (Systema Vegetabilium 6:61. 1820). TROPICOS (23 Aug 2006) cited *Funk 2* (Venezuela) as the type, but a copy of the protologue could not be located. Specimens were not found on either of two visits to P.

Gonolobus pauciflorus Spreng., Syst. veg. 1:846. 1824. Type: HISPANIOLA: 'St. Domingue,' *Bertero s.n.* (lectotype, designated by Krings 2006: P!; isolectotype: G-DC [IDC microfiche Candolle Prodromus Herbarium, fiche # 1543!]). ≡ *Matelea pauciflora* (Spreng.) Woodson, Ann. Missouri Bot. Gard. 28:226. 1941.

Gonolobus pubescens Griseb., Fl. Brit. W.I. 420. 1862. Type: JAMAICA. *Macfadyen s.n.* (holotype: GOET!; isotype: K!) ≡ *Matelea pubescens* (Griseb.) Krings, **comb. nov.**

Gonolobus rhamnifolius Griseb., Fl. Brit. W.I. 420. 1862. Type: JAMAICA, *Alexander s.n.* (holotype: GOET!) ≡ *Matelea rhamnifolia* (Griseb.) Krings, Sida 21:1515. 2005.

Gonolobus sintenisii Schltr., Symb. antill. 1(2):288. 1899. Type: PUERTO RICO: Sierra de Luquillo, Jiménez Mts., 9 Jul 1885 (fl), *Sintenis 1354* (lectotype, designated by Krings 2008: HBG!; isolectotypes: BM!, G!, GH!, K!, US!). ≡ *Matelea sintenisii* (Schltr.) Woodson, Ann. Missouri Bot. Gard. 28:226. 1941.

Gonolobus stipitatus Alain, Phytologia 64:345. 1988, nom. illeg.; non *Gonolobus stipitatus* Morillo, 1987. Type: HAITI: Massif du Nord, St. Louis du Nord, Morne Baron, 950 m, 20 Aug 1925, *Ekman H4693* (holotype: S!; isotypes: B!, US!) = *Matelea crispiflora* (Urb.) Jiménez, Rhodora 62:238. 1960.

See discussion under *Gonolobus haitiensis*.

Gonolobus tigrinus Griseb., Mem. Amer. Acad. Arts 8:520. 1863. Type: CUBA: Holguín, 19 Mar, *Wright 1667* (holotype: GOET, n.v.; syntypes: MO [image online!], G!, GH!, K!). ≡ *Matelea tigrina* (Griseb.) Woodson, Ann. Missouri Bot. Gard. 28:226. 1941.

Gonolobus tigrinus Griseb. var. *angustifolius* Griseb., Cat. pl. Cub. 177. 1866. TYPE: CUBA: *Wright s.n.* (HOLOTYPE: location unknown) = *Matelea grisebachiana* (Schltr.) Alain, Mem. Soc. Cub. Hist. Nat. "Felipe Poey" 22:120. 1955.

See *Gonolobus grisebachianus*

Gonolobus variifolius Schltr., Symb. antill. 1(2):286. 1899. TYPE: PUERTO RICO. Sierra de Luquillo, Jiménez mts., Jun 1885, *Sintenis 1653* (LECTOTYPE: NY!, designated by Krings 2008; ISOLECTOTYPES: G!, GH!, MO!, P!, US!) ≡ *Matelea variifolia* (Schltr.) Woodson, Ann. Missouri Bot. Gard. 28:226. 1941.

Gonolobus virescens Desv. ex Ham., Prodr. pl. Ind. occid. 32. 1825. TYPE: "JAMAICA:" *Desvaux s.n.* (HOLOTYPE: P!).

Rendle (1936) considered *G. virescens* Desv. a *species incerta*. Schlechter (1899) noted that there was likely a label mix-up between *G. stapelioides* and *G. virescens*, and that the latter was likely collected from Tobago and not Jamaica. The morphology of the flowers of *Desvaux s.n.* (P!) places it in Marsdenieae Benth., rather than Gonolobinae.

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INDEX OF NAMES AND TYPES IN WEST INDIAN GONOLOBINAE (APOCYNACEAE: ASCLEPIADOIDEAE), INCLUDING FOURTEEN NEW LECTOTYPIFICATIONS, ONE NEOTYPIFICATION, A NEW NAME, AND A NEW COMBINATION

Alexander Krings

Herbarium, Department of Plant Biology
North Carolina State University
Raleigh, North Carolina 27695-7612, U.S.A.
Alexander_Krings@ncsu.edu

ABSTRACT

Types and their location of deposit are provided for taxa of subtribe Gonolobinae (Apocynaceae: Asclepiadoideae) in the West Indies. The following fourteen taxa are lectotypified: *Gonolobus bayatensis* Urb., *G. broadwayae* Schltr., *G. ciliatus* Schltr., *G. dictyopetalus* Urb. & Ekman, *G. ekmanii* Urb., *G. nipensis* Urb., *G. sintenisii* Schltr., *G. tigrinus* Griseb., *G. tobagensis* Urb., *G. variifolius* Schltr., *Ibatia mollis* Griseb., *Poicilla costata* Urb., *Poicilla tamnifolia* Griseb., and *Poicillopsis crispiflora* Urb. *Gonolobus grenadensis* Schltr. is neotypified. A new name and a new combination in *Matelea* Aubl. are respectively proposed for *Jacaima parvifolia* Proctor and *J. costata* (Urb.) Rendle var. *goodfriendii* Proctor.

RESUMEN

Se aportan tipos y su localización de taxa de la subtribu Gonolobinae (Apocynaceae: Asclepiadoideae) en las Indias Occidentales. Se lectotipifican los siguientes catorce taxa: *Gonolobus bayatensis* Urb., *G. broadwayae* Schltr., *G. ciliatus* Schltr., *G. dictyopetalus* Urb. & Ekman, *G. ekmanii* Urb., *G. nipensis* Urb., *G. sintenisii* Schltr., *G. tigrinus* Griseb., *G. tobagensis* Urb., *G. variifolius* Schltr., *Ibatia mollis* Griseb., *Poicilla costata* Urb., *Poicilla tamnifolia* Griseb., y *Poicillopsis crispiflora* Urb. Se neotipifica *Gonolobus grenadensis* Schltr. Se propone un nombre y una combinación nueva en *Matelea* Aubl. para *Jacaima parvifolia* Proctor y *J. costata* (Urb.) Rendle var. *goodfriendii* Proctor respectivamente.

INTRODUCTION

Subtribe Gonolobinae (Apocynaceae: Asclepiadoideae) comprises about fifty species in the West Indies, here defined to include the Greater and Lesser Antilles, the Bahamas, Trinidad and Tobago, Aruba and the Netherland Antilles, and the Cayman Islands. Evidence from the chloroplast (Rapini et al. 2003; Liede-Schumann et al. 2005; Rapini et al. 2006; Krings et al. 2008) and nuclear genomes (Krings et al. 2008) supports the monophyly of Gonolobinae. Generic circumscriptions remain poorly defined and it is likely that the broad concept of *Matelea* Aubl. sensu Woodson (1941) is not monophyletic. Genera referred to the subtribe with representation in the region include *Fischeria* DC., *Gonolobus* Michx., *Matelea* (incl. *Ibatia* Decne., *Jacaima* Rendle, *Poicilla* Griseb., *Poicillopsis* Schltr., *Ptycanthera* Decne.), *Macroscepis* Kunth, and *Metalepis* Griseb. (Fontella & Schwarz 1981a; Kunze 1995; Liede 1997; Morillo 1997; Rapini et al. 2003; Liede-Schumann et al. 2005; Rapini et al. 2006). Subtribal position has been most controversial for *Metalepis*, which some workers have also placed within in a broad concept of *Cynanchum* L. (Woodson 1941; Spellman 1975; Sundell 1981). Recent evidence places it basal to a well-supported Metastelmatinae-Oxypetalinae-Gonolobinae clade (Liede & Kunze 2002; Liede-Schumann et al. 2005). The last regional treatment of Gonolobinae is now over 100 years old (Schlechter 1899) and a number of new species have been described by various workers, including Britton, Krings, Liogier, Proctor, Spellman, Urban, and Woodson (see Krings 2005b, 2006, 2007, as well as the present study). Recent effort as part of a larger systematic study of Gonolobinae and treatment for the *Flora de la República de Cuba* (Krings 2005a–d, 2006, 2007; Krings et al. 2005; Krings & Fantz 2006; Krings & Saville 2007), has revealed that a number of lectotypifications and neotypifications are necessary. Publishing and compiling these designations separately allows for greater discussion of some issues than is possible in a flora format. The provision of a comprehensive index to all names in West Indian Gonolobinae seems additionally useful considering the scattered nature of the literature and historical errors in citation.

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Fourteen lectotypes and one neotype are designated here. A new name and a new combination in *Matelea* are proposed for *Jacaima parvifolia* Proctor and *J. costata* (Urb.) Rendle var. *goodfriendii* Proctor.

METHODS

Names in West Indian Gonolobinae were compiled from searches of the TROPICOS database (http://www.tropicos.org) for species with West Indian types, as well as from review of pertinent literature (i.e., Grisebach 1862, 1866; Duss 1897; Schlechter 1899; Millspaugh 1902; Boldingh 1909, 1914; Woodson 1941; Moscoso 1943; Cheesman 1947; Alain 1957; Gooding et al. 1965; D'Arcy 1967; Adams 1972; Little et al. 1976; Correll & Correll 1982; Proctor 1984; Howard 1989b; Nicolson 1991; Liogier 1994, 1995; Fournet 2002; Acevedo-Rodríguez 2005). Protologues were compiled from works held at the North Carolina State University Libraries or obtained through inter-library loans. Subsequently, queries were made to ninety institutions known to house West Indian collections—of which sixty-five responded with either loans, digital images, or negative search results (see Acknowledgments). Visits were also undertaken to BM, BSC, DUKE, HAC, HAJB, IJ, K, UCWI, UPRRP, US, and P.

Nearly half of the species names in West Indian Gonolobinae can be attributed to three German workers: August Heinrich Rudolf Grisebach (1814–1879), Friedrich Richard Rudolf Schlechter (1872–1925), and Ignatz Urban (1848–1931). The former worked from the University of Göttingen (GOET) and the latter two from the Botanical Garden and Museum Berlin-Dahlem (B).

The general philosophy followed herein, is that for taxa described by Grisebach, applicable specimens judged original material at GOET are considered holotypes—although, in a strict sense, Grisebach did not designate them as such, although his use of them is evident by his notes and annotations. However, typification of Grisebach names based on collections by Charles Wright (1811–1885) can be problematic, as collections cited under a single collection number frequently represent gatherings from different localities and different times (Howard 1986, 1989a). The philosophy adopted herein is that Grisebach names based on Wright collections should be lectotypified when (1) it can be shown that specimens distributed under a single number represent gatherings from different localities at different times, and/or (2) no specimen of a Wright number remains extant at GOET. When it cannot be shown that gatherings came from different localities and different times, duplicates of a Wright number designated lectotype are considered isolectotypes (see Krings & Fantz 2006). When it can be shown that gatherings came from different localities and different times, duplicates of a designated lectotype are treated as syntypes.

Urban described West Indian taxa largely based on specimens received by him from Erik Ekman (Cuba and Hispaniola), William Harris (Jamaica), and Walter Elias Broadway (Trinidad, Tobago, and Grenada). For these taxa, holotypes are presumed to have remained at B until their destruction in a fire in World War II. Thus, lectotypes are chosen for Urban names from duplicates of numbers cited in his protologues.

RESULTS

Overview.—Names of novelties in West Indian Gonolobinae can be attributed to seventeen workers (Table 1). The majority of taxa were described during four phases of intensive interest in the region that occurred at ca. 20–30 yr intervals over the past 140 yrs. The first phase was dominated by Grisebach and based on the collections of Wullschlagel (Antigua), Charles Wright (Cuba), Imray (Dominica), and Alexander, Higson, Macfadyen, and Purdie (all Jamaica). Important works resulting from activity during this phase include the *Flora of the British West Indian Islands* (Grisebach 1862) and the *Catalogus Plantarum Cubensium* (Grisebach 1866). The second phase was dominated by the activity of Schlechter—based primarily on collections by Broadway (Grenada; Trinidad & Tobago), Eggers (Tobago), Poiteau (Haiti), Sintenis (Puerto Rico), and Wright (Cuba)—and Urban—based primarily on the collections of Broadway (Tobago), Buch (Haiti), Ekman (Cuba & Hispaniola), and Harris (Jamaica). The most important relevant work resulting from this later period of activity is Urban's multi-volume *Symbolae Antillanae* (1898–1928). The third phase was dominated by Liogier (a.k.a. Hermano Alain), who published more West Indian Gonolobinae novelties based on his own collections than any other worker before or since. Additional species described by Liogier are based on collections

TABLE 1. Authors and numbers of novelties at the species rank in West Indian Gonolobinae, based on types from the region.

Author(s)	No. of spp. names published	Author(s)	No. of spp. names published
Alain [Hno.], "A.H. Liogier"	8	Proctor, G.R.	1
Bertoloni, A.	1	Richard, A.	1
Britton, N.L. and P.G. Wilson	1	Schlechter, F.R.R.	9
Decaisne, J.	3	Spellman, D.L.	1
Ekman, E.	1	Sprengler, C.P.J.	2
Grisebach, A.H.R.	12	Urban, I.	9
Hamilton, W.	1	Vahl, M.	2
Jacquin, von, N.	1	Woodson, Jr., R.E.	3
Krings, A.	10		

by Ekman (Hispaniola) and Howard (Dominican Republic). Important works resulting from his efforts or contributions include floras of Cuba, Hispaniola, and Puerto Rico (Alain 1957; Liogier 1994, 1995). The fourth phase of interest is the result of current efforts undertaken by the present author (Krings 2005b, 2006, 2007). New discoveries during this phase are based on collections by Eggers (Dominica), Ekman (Hispaniola), Graveson (St. Lucia), Krings and Springer (St. Vincent), Liogier (Dominican Republic), Marcano and Jiménez (Dominican Republic), and Quentin (Guadeloupe). No new names in West Indian Gonolobinae resulted from R.A. Howard's efforts toward his *Flora of the Lesser Antilles* (Howard, 1989b).

List.—Names are listed index style and include legitimate, illegitimate, and misapplied names. They are arranged strictly alphabetically by basionym or combination. The most recent combination for a respective name follows the basionym (≡). Currently accepted names are in bold or specified under "Notes." Under the name, the locality and/or collector the type is given as it appears in the protologue. Type specimens seen and verified by the author are indicated by an exclamation point ('!') following the herbarium of deposit. The very few specimens not seen are indicated by 'n.v.' (*non vidi*). 'Loc. not cited' signifies that the herbarium of deposit was not indicated in the protologue. Herbarium abbreviations follow Index Herbariorum (Holmgren & Holmgren 1998–present). Book abbreviations follow TL-2 (Stafleu & Cowan 1976–1988) and journal abbreviations B-P-H (Lawrence et al. 1968) and B-P-H/S (Bridson & Smith 1991). Author abbreviations follow Brummitt and Powell (1992).

Asclepias maritima Jacq., Enum. Syst. Pl. 17. 1760. ≡ **Matelea maritima** (Jacq.) Woodson, Ann. Missouri Bot. Gard. 28:222. 1941.

Protologue: Neither specimens, nor locality cited.

Type: Herbar. Du Jacquin, 2 Insulae Caribaea, De Ponthieu (LECTOTYPE designated by Krings & Saville 2007: BM!).

Notes: Only a single sheet of *Asclepias maritima* Jacq. was located that could qualify as belonging to the original material. Eight fragments, all *Asclepias maritima*, are mounted on a single sheet held at BM and barcoded (BM000834432). A handwritten note on the top left of the back of the sheet reads "Herbar. Du Jacquin." followed by "2 Insulae Caribaeae. De Ponthieu." Based on the note, the fragments appear to represent two elements, but they cannot be delineated. A dehisced follicle is mounted along with leaves in relatively good condition and a few flowers in poor condition. Fruits and flowers are not mentioned by Jacquin in the protologue, and these elements may represent the collection later combined with the vegetative fragment used for the protologue. Considering that this sheet appears to represent the only remaining collection of *Asclepias maritima* from the herbarium of Jacquin, it was designated lectotype by Krings and Saville (2007).

Cynanchum denticulatum Vahl, Eclog. Amer. 2:23. 1798. ≡ *Matelea denticulata* (Vahl) Fontella & E.A. Schwarz, Bol. Mus. Bot. Munic. 46:4. 1981.

Protologue: "Habitat in Guiana. von Rohr," loc. not cited.

Type: Guiana, *von Rohr120* (HOLOTYPE: C [IDC microfiche photo: Vahl herbarium nr. 17:III, 1!])

Notes: Most recent authors have accepted this entity under the name *Matelea denticulata* (Vahl) Fontella & E.A. Schwarz. However, in a recent phylogenetic analysis based on chloroplast and nuclear data, the taxon emerged in a clade of *Gonolobus* s.l. (Krings et al. 2008) and should be recognized as *Gonolobus denticulatus* (Vahl) W.D. Stevens in a broad interpretation of the genus.

Cynanchum hirsutum Vahl, Eclog. Amer. 2:24. 1798. ≡ **Matelea hirsuta** (Vahl) Woodson E.E. Cheesman, Fl. Trinidad 2:170. 1947.

Protologue: "Habitat in insula Trinitatis. von Rohr," loc. not cited.

Type: Trinidad, *von Rohr 92* (HOLOTYPE: C [IDC microfiche photo: Vahl herbarium nr. 17:III, 3!; ISOTYPE: BM!).

Notes: An annotation on *von Rohr 92* indicates that it was studied by Ignatz Urban.

Cynanchum maritimum (Jacq.) Jacq., Select. Stirp. Amer. Hist. 83, t. 56. 1763. ≡ **Matelea maritima** (Jacq.) Woodson, Ann. Missouri Bot. Gard. 28:222. 1941.

Notes: Some authors have mistakenly attributed the combination in *Cynanchum* to Linnaeus' *Syst. Nat.* (1767). However Linnaeus (1767) clearly referenced Jacquin (1763). In *Syst. Nat.* (1767), he wrote: "C. caule volubili, fol. cordatis hirsutis subtus tomentosis, pedunc. Aggregatis. Mant. 54." The *Mantissa plantarum* (Mant.) was published originally as an appendix to volume 2 of his *Syst. Nat.* (1767). In the *Mantissa*, Linnaeus (1767) provides further detail, referring to 'Jacq. *amer.* 86, t. 56,' and describing corollas of *C. maritimum* as 'atropurpurea.' Although *C. maritimum* is described on pages 83 and 84 in Jacquin's *Select. Stirp. Amer. Hist.* (1763), rather than on page 86 as cited by Linnaeus (1767), the illustration reference (plate 56) is correct and is not inconsistent with plants known most recently as *Matelea maritima* in the West Indies. Thus, it is clear that Linnaeus accepted Jacquin's combination and was not himself proposing a new one. Continued citation of *Cynanchum maritimum* L. is incorrect.

See *Asclepias maritima* Jacq.

Cynanchum maritimum (Jacq.) L., Syst. Nat. 2:192. 1767, err. cit. [=*C. maritimum* (Jacq.) Jacq., see above].

Notes: Linnaeus (1767) never made this combination mistakenly attributed to him by subsequent workers.

Cynanchum rostratum Vahl, Symb. Bot. 3:45. 1794. ≡ **Gonolobus rostratus** (Vahl) Schult. in Roemer & Schultes, Syst. Veg. 6:61. 1820.

Protologue: "In insula Trinitatis legit Dn. v. Rohr," loc. not cited.

Type: Trinidad, (von Rohr?) Hb. Liebmann (HOLOTYPE: C [IDC microfiche photo: Vahl herbarium nr. 17:III, 5!]; ISOTYPE: BM!).

Notes: Although Stafleu and Cowan (1986) noted that "Vahl's *Symbolae Botanicae* are based on the Forsskål material at C," *Cynanchum rostratum* is not listed in the index accompanying the IDC microfiche of the Forsskål herbarium. However, there is a specimen in the Vahl herbarium corresponding to *Cynanchum rostratum*. The specimen label identifies it as having been part of the Hb. Liebmann at some point, however the hand, identifying the collection as *Cynanchum rostratum*, belongs to Vahl. Von Rohr is not indicated on the label.

Cheesman (1947) mistakenly considered "*Gonolobus rostratus* R.Br. sens. Griseb Fl. 420" a synonym of "*Matelea viridiflora* (G.F.W. Meyer) Woods." However, the latter clearly corresponds to *Matelea denticulata* (Vahl) Fontella & E.A. Schwarz based on Cheesman's description (e.g., "cal[yx] lobes lanceolate," "corolla [...] lobes ovate," "anthers without dorsal appendages") and not to *Gonolobus rostratus* sensu Grisebach (1862) (e.g., "calyx [...] segments ovate," "corolla [...] segments lanceolate-linear"). Grisebach's (1862) taxon (also from Trinidad) is clearly referable to *G. rostratus* (Vahl) Schult. The two taxa are difficult to confuse by anyone familiar with them. The combination in *Gonolobus* is to be attributed to Schultes as Robert Brown never made the combination erroneously attributed to him by some authors such as Grisebach (1862) and Schlechter (1899).

Cynanchum stellatum Vell., Fl. Flumin. 121; 3, t. 80. 1829. ≡ **Fischeria stellata** (Vell.) E. Fourn. in Mart., Fl. Bras. 6:301. 1885.

Protologue: "Habitat silvis maritimis," loc. not cited.

Type: Vell., Fl. Flum. 121; 3, t. 80. 1829. (LECTOTYPE, designated as type by Murphy 1986).

Cynanchum viridiflorum G. Mey., Prim. Fl. Esseq. 141. 1818, nom illegit., non Sims, 1817.
Protologue: "in fruticetis plantationis Hamburg," loc. not cited.
Type(s): The type could not be located.
Notes: A synonym of *Cynanchum denticulatum* Vahl fide Howard (1989b).

Fischeria cincta Griseb., Fl. Brit. W.I. 421. 1862. ≡ *Gonolobus cinctus* (Griseb.) Benth. & Hook. f. ex B.D. Jacks., Index Kewensis 2:1054. 1895.
Protologue: "Jamaica!, *Higson*," loc. not cited.
Type: Jamaica, *Higson s.n.* (HOLOTYPE: K!).
Notes: A synonym of *Gonolobus stapelioides* Desv. ex Ham. fide Adams (1972).

Fisheria havanensis Decne. in DC., Prodr. 8:601. 1844.
Protologue: "in insula Cuba (Ramon de la Sagra, n. 556). (v.s.h. DC.)."
Type: Cuba, *Ramon de la Sagra 555* [*556* fide Decne. in DC., Prodr. 8:601.] (HOLOTYPE: G-DC [IDC microfiche Candolle Prodromus Herbarium, fiche # 1542!]), photos at MO, n.v., F, n.v.).
Notes: A synonym of *Fischeria scandens* DC. fide Murphy (1986).

Fischeria multiflora Decne. in DC., Prodr. 8:601. 1844.
Protologue: "in Brasilia (cl. Martius) (v.s.h. reg. monac.)."
Type: Brazil, *Martius s.n.* (HOLOTYPE: M, n.v.; ISOTYPE: M, n.v.).
Notes: Murphy (1986) considered *F. multiflora* Decne. a synonym of *F. stellata* (Vell.) E. Fourn. The latter is the only species of *Fischeria* she recognized from Trinidad.

Fischeria multiflora Griseb., Fl. Brit. W.I. 421. 1862, err.cit. [=*F. multiflora* Decne.].
Notes: In contrast to Grisebach himself (loc. cit.), Schlechter (1899) believed that Grisebach's *F. multiflora* did not belong to Decaisne's Brazilian species by the same name, but rather to *F. havanensis* Decne. Cheesman (1947) accepted this as well. Murphy (1986) considered *F. havanensis* Decne. a synonym of *F. scandens* DC., but did not recognize this taxon from Trinidad, the locality from which Grisebach (loc. cit) cited his *F. multiflora* (based on Purdie and Crueger collections). Murphy (1986) recognized only *F. stellata* (Vell.) E. Fourn.—under which she submerged *F. multiflora* Decne.—from the island.

Fischeria scandens DC., Cat. Pl. Horti Monsp. 112. 1813.
Protologue: "Hab. verosimiliter in America meridionali. Habuimus ex horto Madritensi," "h. monsp. inedit. t. 67."
Type: America meridionali, hort. monsp. ined., t. 67 (HOLOTYPE: MPU, n.v.).
Notes: *Fischeria scandens* is the only species of *Fischeria* recognized by Murphy (1986) from the Greater Antilles.

Fischeria stellata (Vell.) E. Fourn. in Mart., Fl. Bras. 6:301. 1885.
See *Cynanchum stellatum* Vell.

Gonolobus absalonensis Krings, Syst. Bot. 32:181. 2007.
Protologue: "Martinique. Absalon, Près la cascade, Mai 1910 (fl), Herb. d'Alleizette *s.n.* [*4801*?] (HOLOTYPE: L!)."
Type: Martinique, Absalon, Près la cascade, May 1910, Herb. d'Alleizette *s.n.* [*4801*?] (HOLOTYPE: L!).

Gonolobus bakeri Schltr. in Urban, Symb. Antill. 7(3):341. 1912.
Protologue: "Hab. in Cuba cult. in Santiago de las Vegas: *C.F. Baker n. 7286*, flor. m. Majo 1907," loc. not cited.
Type: Location of type is unknown. No additional matching material was located from which a lectotype or neotype could be designated. See Krings (2008) for a discussion of this taxon.

Gonolobus bayatensis Urb., Symb. Antill. 9(3):420. 1925. ≡ **Matelea bayatensis** (Urb.) Woodson, Ann. Missouri Bot. Gard. 28:226. 1941.

Protologue: "Prov. Oriente prope Bayate, m. Oct. flor.: Arth. Engström in herb. Ekman n. 3056," loc. not cited.
Type: Cuba, Oriente, Bayate, 9 Oct 1914, *Engström 3056* (LECTOTYPE, here designated: S!; ISOLECTOTYPE: NY!).
Notes: Two sheets of *Engström 3056* are extant—one at S and one at NY. The sheet at S is superior in condition to the NY sheet, exhibiting much more floral and vegetative material and is therefore designated lectotype. See Krings (2005c) for additional notes on this species.

Gonolobus bicolor (Britton & P.Wilson) Urb., Symb. Antill. 9(3):421. 1925. ≡ **Matelea bicolor** (Britton & P. Wilson) Woodson, Ann. Missouri Bot. Gard. 28:236. 1941.
See *Marsdenia bicolor* Britton & P. Wilson.

Gonolobus broadwayae Schltr. in Urb., Symb. Antill. 7(3):340. 1912.
Protologue: "in Trinidad, ad St. Clair Experiment Station inter Bambusas volubilis: *W.E. Broadway n. 2743*," loc. not cited; 'ad Santa Cruz: *López* (Herb. Broadway n. 2419),' loc. not cited.
Type: Trinidad, *López 2419* (LECTOTYPE, here designated: Z!).
Notes: Of the two syntypes cited in the protologue, only *López 2419* (Z) appears to be extant. *Gonolobus broadwayae* Schltr. is a synonym of *G. rostratus* (Vahl) Schult.

Gonolobus ciliatus Schltr. in Urban, Symb. Antill. 1(2):282. 1899.
Protologue: "Tobago, in silvis prope Frenchfield, alt. 400 ped., Oct.: *Eggers 5561*," loc. not cited; 'Trinidad, prope La Ventilla: *Crüger* s.n.,' loc. not cited; 'Venezuela,' loc. not cited.
Type: Tobago, *Eggers 5561* (LECTOTYPE, here designated: P!; ISOLECTOYPE: UCWI!).
Notes: Unidentified as a type, *Eggers 5561* had been filed at P with *Matelea denticulata* (Vahl) Fontella & E.A. Schwarz. The *Crüger* specimen could not be located. *Gonolobus ciliatus* Schltr. is a synonym of *G. denticulatus* (Vahl) W.D. Stevens.

Gonolobus cinctus (Griseb.) Benth. & Hook. f. ex B.D. Jacks., Index Kewensis 1:1054. 1895.
See *Fischeria cincta* Griseb.

Gonolobus cinctus (Griseb.) Benth., Gen. Pl. 2:750. 1876, err.cit. [= **Gonolobus stapelioides** Desv. ex Ham.].
Notes: This combination is not valid, as the epithet of the basionym—*Fischeria cincta* Griseb.—was not definitely associated with the genus *Gonolobus*.

Gonolobus denticulatus (Vahl) W.D. Stevens, Phytologia 64:334. 1988.
See *Cynanchum denticulatum* Vahl.

Gonolobus dictyopetalus Urb. & Ekman, Ark. Bot. 20A(5):41. 1926. ≡ **Matelea dictyopetala** (Urb. & Ekman) Krings, J. Bot. Res. Inst. Texas 2:130. 2008.
Protologue: Haiti, "Massif de la Selle in Morne Cabaio ad Jardin Bois [...] n. H. 1625," loc. not cited.
Type: Haiti, Massif de la Selle, Morne Cabaio, ca. 1900 m, 24 Aug 1924, *Ekman H 1625* (LECTOTYPE, here designated: S!; ISOLECTOTYPE: IJ! – fragment [single leaf]).
Notes: Two sheets of *Ekman H 1625* are known—one at IJ and another at S. Whereas the sheet at IJ consists of a stem fragment with a single leaf (plus several more leaf fragments and a flower bud in the fragment pocket), the sheet at S (determined in Urban's hand) consists of numerous leaves and flowers and is in good condition. Ekman specimens were sent to Urban at B for critical study (Howard, 1952; Nordenstam et al., 1994). Nordenstam et al. (1994) noted that Urban was to identify and publish on the work of Ekman and return the principal (full) set of vascular and non-vascular plants to Stockholm (S). Nordenstam et al. (1994) also noted that it is obvious that Urban returned the original specimens to Stockholm as many Ekman sheets are annotated as types in Urban's handwriting. Urban could keep one duplicate of the material upon which any of his and Ekman's publications were based (Nordenstam et al., 1994). Urban published a number of names

in West Indian Gonolobinae based on Ekman material and it can be assumed that holotypes were kept at B. However, all of Gonolobinae types at B were destroyed in World War II, necessitating lectotypification.

Gonolobus domingensis Alain, Moscosoa 1(3):46. 1978. ≡ **Matelea domingensis** (Alain) Krings, Sida 21:2081. 2005.
Protologue: "Loma Isabel de Torres, Puerto Plata [...] *Alain & Perfa Liogier 13780* (SDM, NY); en bosque, id. *A. & P. Liogier & N. Melo 23348* (SDM)."
Type: Dominican Republic, estribo sur del Isabel de Torres, Puerto Plata, alt. 750 m, 16–17 Aug 1975 (fl), *Alain & Perfa Liogier 23780* (LECTOTYPE designated by Krings 2005d: JBSD!).
Notes: See Krings (2005d) for a detailed discussion of lectotypification of this taxon.

Gonolobus dussii Krings, Syst. Bot. 32:183. 2007.
Protologue: "Guadeloupe. Chemin de la Soufrière, alt. 500 m, *Quentin 732* (HOLOTYPE: P!-fl; ISOTYPE: GH!-fl)."
Type: Guadeloupe, Chemin de la Soufrière, alt. 500 m, *Quentin 732* (HOLOTYPE: P!-fl; ISOTYPE: GH!-fl).

Gonolobus ekmanii Urb., Symb. Antill. 9(3):422. 1925. ≡ **Matelea ekmanii** (Urb.) Woodson, Ann. Missouri Bot. Gard. 28:226. 1941.
Protologue: "Prov. Oriente in Sierra Maestra inter Rio Yara et Rio Palmamocha cr. 1300 m. alt., m. Jul. flor., n. 14453," loc. not cited.
Type: Cuba, *Ekman 14453* (LECTOTYPE, here designated: S!; ISOLECTOTYPE: NY!).
Notes: Two sheets of *Ekman 14453* are held at S. One sheet holds a nicely, openly pressed flower in its fragment pocket. Considering that the condition of both sheets is otherwise comparable, the sheet with the openly pressed flower in the fragment pocket is here designated lectotype. As accession numbers are the same on both sheets, the lectotype can be identified by the label header: "Mus. Botan. Stockholm. Plantae Indiae Occidentalis N:o 14453" [sic].

Gonolobus floccosus Bertol., Opusc. Sci. 4:225. 1823.
Protologue: "[...] ex Guadalupa, et Portorico," Anonymous (loc. not cited).
Type: Guadeloupe, *Anonymous s.n.* (HOLOTYPE: BOLO!).
Notes: A synonym of *Matelea maritima* (Jacq.) Woodson.

Gonolobus grenadensis Schltr. in Urban, Symb. Antill. 7(3):339. 1912.
Protologue: "in Grenada ad Annandale, *W.E. Broadway n. 3477*," loc. not cited.
Type: Grenada, St. Mark Parish, Wooded hillsides near Victoria, elev. 100–300 ft, 24 Nov 1957, *G.R. Proctor 17225* (NEOTYPE, here designated: IJ!).
Notes: Based on Schlechter's (1912) description, *Gonolobus grenadensis* Schltr. is a synonym of *Gonolobus denticulatus* (Vahl) W.D. Stevens. Schlechter (1912) considered it a close relative to *G. ciliatus* Schltr. (also a synonym of *G. denticulatus*), from which he distinguished it only by larger leaves and flowers. Howard (1989b) also treated *G. grenadensis* as a synonym of *G. denticulatus*, although confusing it with *G. martinicensis* in key and description (though not in illustration). Unfortunately no original material of *G. grenadensis* could be located. *Proctor 17225* (IJ) appears to be the only extant specimen of this taxon from Grenada. It is here designated neotype.

Gonolobus grisebachianus Schltr. in Urban, Symb. Antill. 1(2):287. 1899. ≡ **Matelea grisebachiana** (Schltr.) Alain, Mem. Soc. Cub. Hist. Nat. "Felipe Poey" 22:120. 1955.
Protologue: "Cuba, loco speciali haud indicato: *Wright s.n.*," loc. not cited.
Type: Location of type is unknown. No additional matching material was located.

Gonolobus haitiensis P.T. Li, J. South China Agric. Univ. 14(1):58. 1993.
Type: Haiti, Massif du Nord, St. Louis du Nord, Morne Baron, 950 m, 20 Aug 1925, *E.L. Ekman 4693* (HOLOTYPE: S!; ISOTYPES: B!, US!).

Notes: A nomen nov. for *Gonolobus stipitatus* Alain, Phytologia 64:345. 1988, non Morillo, 1987. Krings (2008) considered *G. haitiensis* a synonym of *Matelea crispiflora* (Urb.) J. Jiménez Alm.

Gonolobus iyanolensis Krings, Syst. Bot. 32:185. 2007.
Protologue: "St. Lucia. Gros Piton, 9 Aug 1996 ["9/8/76"] (fl), *Roger Graveson 107* (HOLOTYPE: GH!)."
Type: St. Lucia, Gros Piton, 9 Aug 1996 ["9/8/76"], *Roger Graveson 107* (HOLOTYPE: GH!).
Notes: Roger Graveson noted that the collection date is incorrect on the label of the type and should be 9 Aug 1996 instead (Graveson, pers. comm.).

Gonolobus jamaicensis Rendle, J. Bot. 74:345. 1936.
Type: Jamaica, near Vinegar Hill, climbing up trees to height of 20 ft, 4200 ft elev., 5 Jun 1896, *Harris 6368* (HOLOTYPE: BM!).
Notes: *Gonolobus jamaicensis* was proposed by Rendle as a nomen novum for the Jamaican endemic taxon Schlechter (1899) attributed to *G. rostratus* (Vahl) R.Br. Robert Brown never made the combination attributed to his Memoirs of the Wernerian Natural History Society 1:35. 1810. The true *Gonolobus rostratus* (Vahl) Schult. is known only from Trinidad in our area and is based on the type of *Cynanchum rostratum* Vahl. Because Rendle corrected a misapplication, his name—*G. jamaicensis*—is a new species name, not a nomen novum as he incorrectly stated. A nomen novum is an avowed substitute (replacement name) for a validly published but illegitimate name, the type of which would be the same as that of the name which it replaced.

Gonolobus maritimus (Jacq.) R.Br., Mem. Wern. Nat. Hist. Soc. 1: 24. 1810. ≡ **Matelea maritima** (Jacq.) Woodson, Ann. Missouri Bot. Gard. 28:222. 1941.
See *Asclepias maritima* Jacq.

Gonolobus maritimus (Jacq.) R.Br. ex Schult. in Roemer & Schultes, Syst. Veg. 6:59. 1820, err. cit. [=*G. maritimus* (Jacq.) R.Br.]
Notes: Brown (1810) validly and effectively published the combination *Gonolobus maritimus* (Jacq.) R.Br. The sometimes mistakenly cited combination *Gonolobus maritimus* (Jacq.) R.Br. ex Schult., Syst. Veg. 6:59. 1820, is an error in citation as Schultes clearly accepted Brown's combination, correctly additionally citing Jacquin.
See *Asclepias maritima* Jacq.

Gonolobus martinicensis Decne. in De Candolle, Prodr. 8:595. 1844.
Protologue: "in Martinicae sylvis umbrosis, (cl. *Plée.*) *Tourimibi* Caribeorum *Plum. et Surian 821* (v.s.h. Mus. par.)."
Type: Martinique, *Pleé s.n.* (LECTOTYPE designated by Krings 2007: P!).
Notes: Two syntypes were cited in the protologue, but only *Pleé s.n.* (P) could be re-located. *Plum. et Surian 821* could not be found.

Gonolobus membranaceus Schltr. in Urban, Symb. Antill. 1(2):285. 1899.
Protologue: "Haiti, loco speciali haud indicato: *Poiteau s.n.*," loc. not cited.
Type: The location of the type remains unknown. No additional matching material was found.
Notes: *Ekman H4693* (IJ!) is labelled *Gonolobus membranaceus*. The specimen consists of mostly stem and 3–4 leaf fragments held in a fragment pocket. It appears to match *Poicillopsis crispiflora* Urb. *Gonolobus membranaceus* is likely very closely related to *Matelea haitiensis* as, based on the protologues, the two appear to differ only in the shape and apices of the leaf blades and calyx lobes. Additional collections and discovery of the type may prove them synonymous.

Gonolobus nipensis Urb., Symb. Antill. 9(3):421. 1925. ≡ **Matelea nipensis** (Urb.) Woodson, Ann. Missouri Bot. Gard. 28:226. 1941.
Protologue: "Prov. Oriente in Sierra de Nipe ad pedem Loma Mensura in savannis pinetorum umbrosis cr. 725 m. alt., m. Jul. flor.: n. 9710," loc. not cited.

Type: Cuba, Oriente, Sierra de Nipe, Loma Mensura, ca. 725 m, 11 Jul 1919, *Ekman 9710* (LECTOTYPE, here designated: S!; ISOLECTOTYPE: NY!).
Notes: *Ekman 9710* (S) is a superior specimen relative to *Ekman 9710* (NY) in that it bears many more leaves, inflorescences, and flowers. It is here designated lectotype for *Gonolobus nipensis*.

Gonolobus pauciflorus Spreng., Syst. Veg. 1:846. 1824. ≡ **Matelea pauciflora** (Spreng.) Woodson, Ann. Missouri Bot. Gard. 28:226. 1941.
Protologue: "Hispaniola, *Bertero*," loc. not cited.
Type: Hispaniola: 'St. Domingue,' *Bertero s.n.* (LECTOTYPE designated by Krings 2006: P!; ISOLECTOTYPE: G-DC [IDC microfiche Candolle Prodromus Herbarium, fiche # 1543!]).
Notes: Bertero collections were among specimens in the fragmented Sprengel collection acquired by B in 1890, but no Bertero specimen corresponding to *G. pauciflorus* was found extant at that institution. As neither extant duplicate of *Bertero s.n.* at either G-DC or P corresponding to *G. pauciflorus* bears the hand of Sprengel and as no other Bertero material corresponding to the taxon has been located at the other institutions queried (see Acknowledgments), it is assumed that the holotype was destroyed. Consequently, having been able to examine the specimen at P, but only the microfiche of the specimen at G-DC, Krings (2006) designated the sheet at P lectotype for *G. pauciflorus*.

Gonolobus pubescens Griseb., Fl. Brit. W.I. 420. 1862. ≡ **Matelea pubescens** (Griseb.) Krings, J. Bot. Res. Inst. Texas 2:131. 2008.
Protologue: "Jamaica, *Macf.*," loc. not cited.
Type: Jamaica, *Macfadyen s.n.* (HOLOTYPE: GOET!; ISOTYPE: K!).
Notes: The GOET specimen consists of an unmounted section of stem with five nodes, but only three developed leaves. A fourth developed leaf and a fragment of a fifth are loose in the pocket. A smaller fragment pocket contains floral parts. *Macfadyen s.n.* (K) is a superior specimen relative to *Macfadyen s.n.* (GOET) in bearing many more leaves, as well as an openly pressed flower kept in the fragment pocket. Both the K and GOET specimens are annotated in Grisebach's hand.

Gonolobus rhamnifolius Griseb., Fl. Brit. W.I. 420. 1862. ≡ **Matelea rhamnifolia** (Griseb.) Krings, Sida 21:1515. 2005.
Protologue: "Jamaica!, *Al.*, S. Anns, near Moneague," loc. not cited.
Type: Jamaica, *R.C. Alexander s.n.* (HOLOTYPE: GOET!).
Notes: See Krings (2005a) for a discussion of the morphology of this taxon. The type locality was visited on an expedition to Jamaica by the present author and Dale Suiter in March 2006. However, the area was unfortunately flooded (houses under 10–15 feet of water) and inaccessible. The species was not observed on any of the access roads up to the flooded valley. Dr. George Proctor noted collecting a specimen in a narrow patch of woods between a road and a pasture. The area appears to be in similar condition currently, with many pastures separated from rural roads by narrow patches of woods.

Gonolobus rostratus (Vahl) Schult. in Roemer & Schultes, Syst. Veg. 6:61. 1820.
Notes: Schultes (1820) cited Vahl's protologue of *Cynanchum rostratum* (see above) and attributed the combination in *Gonolobus* to Robert Brown. However, as Brown never made the combination in *Gonolobus* that has been attributed to him, Schultes should be considered the author of the valid combination.
See *Cynanchum rostratum* Vahl.

"*Gonolobus rostratus*" auct. non (Vahl) Schult.: Schlechter in Urb., Symb. Antill. 1:284. 1899.
Notes: Schlechter (1899) mistakenly attributed a Jamaican entity to the name *Gonolobus rostratus* (Vahl) R.Br., for which Rendle later proposed the name *G. jamaicensis* (see above). Robert Brown never made this combination attributed to him (see Memoirs of the Wernerian Natural History Society 1:35. 1810).
See also *Cynanchum rostratum* Vahl.

"*Gonolobus scandens* (Aubl.) Urb.," Repert. Spec. Nov. Regni Veg. 16:151. 1919; nom. illeg.

Notes: Based on an invalid polynomial—*Periploca scandens* Aubl., Histoire des plantes de la Guiane Françoise 2 (Tabl. Nom. Lat.):23. 1775. 260. See Nicolson (1991) for a discussion.

Gonolobus scandens Urb., Repert. Spec. Nov. Regni Veg. 16:151. 1919; nom. illeg.
Notes: A superfluous name and synonym of *Gonolobus martinicensis* Decne. (Prodromus Systematis Naturalis Regni Vegetabilis 8:595. 1844.).

Gonolobus sintenisii Schltr. in Urban, Symb. Antill. 1(2):288. 1899. ≡ **Matelea sintenisii** (Schltr.) Woodson, Ann. Missouri Bot. Gard. 28:226. 1941.
Protologue: "Portorico, Sierra de Luquillo, in regione superiore montis Jimenes in silvis, Jul. 1885: *Sintenis n. 1354*; in silva primaeva montis Andubo prope Adjuntas, Jun. 1886: *Sintenis n. 4643*," loc. not cited.
Type: Puerto Rico, Sierra de Luquillo, Jiménez mts., 9 Jul 1885, *Sintenis 1354* (LECTOTYPE, here designated: HBG!; ISOLECTOTYPES: BM!, G!, GH!, K!, US!).
Notes: Among the syntypes, *Sintenis 1354* (HBG) is chosen as lectotype as the specimen bears flowers in relatively superior condition to the duplicates under this number. The two specimens respectively at G and GH are sterile. The K specimen bears a single flower in bud. Specimens of *Sintenis 4643* could not be located.

Gonolobus stapelioides Desv. ex Ham., Prodr. Pl. Ind. Occid. 32. 1825.
Protologue: "Habitat in fruticetis circa Alfred Hall, prope Scarborough, Tobago, cum *Echite quinquangulare* etc. ubi florentem inveni mense Octobris (V. et S. v.)," loc. not cited.
Type: Jamaica, Portland Parish, 0.5 mi N of Hardwar Gap, uphill from the trail above the "Waterfall," ca. 3900 ft, montane rainforest, vines growing over trailside shrubs and in small forest openings, population J1, 3 Mar 2006, *A. Krings 1395 with D. Suiter and G.R. Proctor* (neotype: P!, designated by Krings 2008; isoneotypes: BM!, IJ!, NCSC!, NY!).
Notes: Schlechter (1899) noted that there was likely a label mix-up between the Jamaican entity *G. stapelioides* and the Tobagoan *G. virescens* Ham. It would indeed be unlikely for *G. stapelioides* to be limited in distribution to Jamaica and Tobago. The taxon is not represented by any other specimens from Tobago. Similarly, *G. virescens* is not known from Jamaica by another specimen. A neotype is proposed as the holotype could not be found.

Gonolobus stellatus Griseb., Fl. Brit. W.I. 420. 1862.
Protologue: "Jamaica!, *Pd.*, Manchester, rare, near Knockpatrick," loc. not cited.
Type: Jamaica, *Purdie s.n.* (HOLOTYPE: GOET!; ISOTYPES: BM!, K!).
Notes: *Purdie s.n.* (K) is the best specimen of the three extant sheets. It bears numerous leaves, inflorescences, and an openly pressed flower. The specimen also bears an annotation in Grisebach's hand. The specimen at BM is also in good condition, bearing a nicely preserved flower. However, this specimen does not bear annotations in Grisebach's hand. The specimen at GOET consists entirely of fragments (two leaves and immature flowers in bud; no stem).

Gonolobus stephanotrichus Griseb., Cat. Pl. Cub. 177. 1866.
Protologue: "Cuba or. (*Wr. 2969* [...]," loc. not cited.
Type: Cuba, 1860–1864, *Wright 2969*(LECTOTYPE, designated by Krings & Fantz 2006: GOET!; SYNTYPES: BM!, BREM!, G!, GH!, HAC!, K!, MO, NY!, P!, UC!, US!).
Notes: The Wright collection of *G. stephanotrichus* at S bears the number 164 and does not appear to be part of the type collection. See Krings and Fantz (2006) for a detailed discussion of the lectotypification of *G. stephanotrichus*.

Gonolobus stipitatus Alain, Phytologia 64(5):345. 1988, nom. illeg.; non *Gonolobus stipitatus* Morillo, 1987. = *Gonolobus haitiensis* P.T.Li, J. South China Agric. Univ. 14(1):58. 1993.
Protologue: "Haiti: On hard limestone, Massif du Nord, St. Louis du Nord, on top of Morne Baron, Jul 20, 1925, *Ekman 4693* (HOLOTYPUS: S)."
Type: Haiti, Massif du Nord, St. Louis du Nord, Morne Baron, 20 Aug 1925, *Ekman H 4693* (HOLOTYPE: S!; ISOTYPES: B!, US!).

"*Gonolobus suberosus*" auct. non (L.) R.Br.: Spreng., Syst. Veg. 1:846. 1824.
Notes: Cited as *Gonolobus suberosus* Spreng. by Schlechter (1899) and Woodson (1941), although Sprengel (1824) clearly cited Robert Brown as author of the combination in *Gonolobus* based on the basionym *Cynanchum suberosum* L. Although the typification of *C. suberosum* L. is complex (Drapalik 1969; Reveal & Barrie 1992) , the basionym has most recently been recognized to apply to the single *Gonolobus* species in the southeastern United States (see Krings & Xiang 2004, 2005). Schlechter (1899) and Woodson (1941) considered Sprengel's *G. suberosus* to be a synonym of what is now known as *Matelea maritima* (Jacq.) Woodson. Sprengel's description is not inconsistent with their decision.

Gonolobus tigrinus Griseb., Mem. Amer. Acad. Arts 8:520. 1863. ≡ **Matelea tigrina** (Griseb.) Woodson, Ann. Missouri Bot. Gard. 28:226. 1941.
Protologue: "[*Wright*] (*1667*)," loc. not cited.
Type: Cuba, Holguín, 19 Mar, *Wright 1667* (LECTOTYPE, here designated: GOET, n.v., fide Howard 1989a; SYNTYPES: MO [image online!], G!, GH!, K!).
Notes: Specimens distributed under *Wright 1667* were collected by Wright from at least two different localities at two different times (GH: "in coffee fields, Josephina, Nov 1"; GOET: "Holguin, 19 Mar"). Krings (2005c) mistakenly stated that Howard lectotypified *G. tigrinus* based on *Wright 1667* at GOET. However, Howard's "lectotypification" (1989a) appeared in a microfiche appendix, not in print, and thus is not effectively published and has no standing in nomenclature. Rankin & Greuter (2000) reported a similar case in Antillean *Aristolochia*.

Gonolobus tigrinus Griseb. var. *angustifolius* Griseb., Cat. Pl. Cub. 177. 1866.
Protologue: "*Wr.* [*Wright*]," loc. not cited.
Type: The location of the type remains unknown. No additional matching material was found.
Notes: This taxon was recognized at the specific rank by Schlechter (1899) as *G. grisebachianus* Schltr.

Gonolobus tobagensis Urb., Repert. Spec. Nov. Regni Veg. 16:37. 1919.
Protologue: "in Tobago in districtu The Widow nominato, m. April. flor, *W.E. Broadway no. 4467* [loc. not cited]."
Type: Tobago, the Widow, 28 Apr 1913, *W.E. Broadway 4467* (LECTOTYPE, here designated: BM!).
Notes: Among the great bulk of collections received by Urban from Erik Ekman (Cuba and Hispaniola) and William Harris (Jamaica), are specimens sent to him by W.E. Broadway from Trinidad, Tobago, and Grenada. Holotypes are presumed to have remained at B until their destruction in a fire in World War II. There is no indication on *Broadway 4467* (BM) that it was seen by Urban, but as the only apparently extant sheet of the number cited by Urban in the protologue, it is here designated lectotype of *G. tobagensis*.

Gonolobus variifolius Schltr. in Urban, Symb. Antill. 1(2):286. 1899. ≡ **Matelea variifolia** (Schltr.) Woodson, Ann. Missouri Bot. Gard. 28:226. 1941.
Protologue: "Portorico, Sierra de Luquillo, in regione media montis Jimenes in fruticetis, Jun. 1885: *Sintenis n. 1653*,' loc. not cited; 'montis Cienega prope Adjuntas, Jun. 1886: *Sintenis n. 4687*," loc. not cited.
Type: Puerto Rico, Sierra de Luquillo, Jiménez mts., Jun 1885, *P. Sintenis 1653* (LECTOTYPE, here designated: NY!; ISOLECTOTYPES: G!, GH!, MO!, P!, US!); *P. Sintenis 4687* (SYNTYPE: K!).
Notes: *Sintenis 1653* (NY) is here designated as lectotype for *Gonolobus variifolius* Schltr. as, unlike the other specimens, it bears a diversity of leaves, a number of inflorescences, and flowers.

Gonolobus viridiflorus Schult. in Roemer & Schultes, Syst. Veg. 6:61. 1820.; nom. illeg., non *G. viridiflorus* Nutt. (1818).
Protologue: "*Meyer*," loc. not cited.
Type: unknown.
Notes: Schultes (1820) clearly cited Meyer's basionym, *Cynanchum viridiflorum*. However, *C. viridiflorum* G. Mey. is illegitimate, being a later homonym of *C. viridiflorum* Sims (1817). The basionym epithet is not available in *Gonolobus* due to the earlier *G. viridiflorus* Nutt. (1818). Most recent authors have accepted this entity

under the name *Matelea denticulata* (Vahl) Fontella & E.A. Schwarz (Boletim do Museu Botanico Municipal 46:4. 1981.), although, as it emerged in a clade of *Gonolobus* s.l. (Krings et al. 2008) the name *G. denticulatus* (Vahl) W.D. Stevens is preferable.

Gonolobus waitukubuliensis Krings, Syst. Bot. 32:187. 2007.
Protologue: "Dominica. In sylvis ad Laudat, Mai 1882 (fl), *Eggers 728* (HOLOTYPE: HBG! [2 sheets]; ISOTYPES: FR!, G!, GH!, JE!, M!, W!, Z!)."
Type: Dominica, in sylvis ad Laudat, May 1882, *Eggers 728* (HOLOTYPE: HBG! [2 sheets]; ISOTYPES: FR!, G!, GH!, JE!, M!, W!, Z!).

Gonolobus youroumaynensis Krings, Syst. Bot. 32:191. 2007.
Protologue: "Orange Hill Estate, roadbank in banana and pigeon pea plantations, uphill from fork in road to the C.W.S.A. water intake site, Kiss-me, 14 Mar 2006 (fl), *Krings 1374 with Springer* (HOLOTYPE: NCSC!; ISOTYPES: GH!, K!, NY!, US!, P!)."
Type: St. Vincent, Orange Hill Estate, roadbank in banana and pigeon pea plantations, uphill from fork in roSad to the Central Water and Sewage Authority water intake site, Kiss-me, 14 Mar 2006, *Krings 1374 with Springer* (HOLOTYPE: NCSC!; ISOTYPES: GH!, K!, NY!, US!, P!).

Holostemma candolleanum Spreng., Syst. Veg. 1:851. 1824, nom. illeg.
Notes: Sprengler (loc. cit.) cited *F. scandens* DC. in synonymy, thus making his name illegitimate. Schlechter (1899) placed Sprengler's name in synonymy under *Fischeria crispiflora* (Sw.) Schltr.—a later homonym of *F. crispiflora* (Sw.) K. Schum.—which he misapplied to the taxon recognized by Murphy (1986) as *F. scandens* DC.

Ibatia maritima (Jacq.) Decne. in De Candolle, Prodr. 8:599. 1844. ≡ **Matelea maritima** (Jacq.) Woodson, Ann. Missouri Bot. Gard. 28:222. 1941.
See *Asclepias maritima* Jacq.

Ibatia mollis Griseb., Cat. Pl. Cub. 177. 1866. ≡ **Matelea mollis** (Griseb.) Woods., Ann. Missouri Bot. Gard. 28:223. 1941.
Protologue: "Cuba occ. - pr. La Concordia (*Wr. 2978*)," loc. not cited.
Type: Cuba, *Wright 2978* (LECTOTYPE, here designated: GH!; SYNTYPES: K!, MO! [image online]).
Notes: See discussion under *Gonolobus tigrinus* regarding problems of typification of Grisebach names based on Wright collections. Unfortunately, there is no extant Wright material of number 2978 at GOET. However, a specimen does exist at GH, which can be designated lectotype following Howard (1989a). Two elements are mounted on the sheet—one with flowers and one with fruits. As fruits were not mentioned in the protologue, the flowering element of *Wright 2978* (GH) is here designated as lectotype for *Ibatia mollis* Griseb. Other combinations include: *Ptycanthera mollis* (Griseb.) Schltr. in Urb., Symb. Antill. 1(2):280. 1899.

Ibatia muricata Griseb., Fl. Brit. W.I. 421. 1862.
Protologue: "Antigua!, *Wullschl.*, Dominica!, *Imr.*; [Guadeloupe! ; Venezuela!]," loc. not cited.
Type: Antigua, Cedar Hall, 1849, *Wullschlagel* (LECTOTYPE designated by Krings & Saville 2007: M! [2 sheets])
Notes: Although not identified as a type, the material at M was the only Wullschlagel specimen from Antigua found in the course of a study by Krings and Saville (2007) and was designated lectotype of *Ibatia muricata*. Grisebach's name is a synonym of *Matelea maritima* (Jacq.) Woodson, Ann. Missouri Bot. Gard. 28:222. 1941.

Jacaima costata (Urb.) Rendle, J. Bot. 74:340. 1936. ≡ **Matelea costata** (Urb.) Morillo, Anales Jard. Bot. Madrid 43:239. 1987 ["1986"].
See *Poicilla costata* Urb.

Jacaima costata (Urb.) Rendle var. *goodfriendii* Proctor, J. Arnold Arbor. 63:290. 1982. ≡ **Matelea costata** (Urb.) Morillo var. **goodfriendii** (Proctor) Krings, **comb. nov.**

Protologue: "St. Ann: Cedar Valley distr., ca. 1.5 mi NE of Cave Valley Square, ca. 2000 ft, *Goodfriend s.n.* (IJ 65657), May 17, 1977 (flowers) (HOLOTYPE), *Goodfriend s.n.* (IJ 66697), Jul 1977 (fruit)."
Type: Jamaica, St. Ann: Cedar Valley distr., ca. 1.5 mi NE of Cave Valley Square, wooded limestone hills, ca. 2000 ft, 17 May 1977, *Goodfriend s.n.* (HOLOTYPE: IJ!); Jul 1977, *Goodfriend s.n.* (PARATYPE: IJ!).

Jacaima parvifolia Proctor, J. Arnold Arbor. 63:291. 1982. = **Matelea proctori** Krings, **nom. nov.**
Protologue: "Clarendon: Broom Hall hills, 1.2 mi SW of Cave Valley Square, 1800–2000 ft, *Proctor 37887*, Jul 9, 1978 (HOLOTYPE)."
Type: Jamaica, Clarendon: Broom Hall hills, 1.2 mi SW of Cave Valley Square, 1800–2000 ft, 9 Jul 1978, *Proctor 37887* (HOLOTYPE: GH!; ISOTYPE: IJ!).
Notes: A new name is required as a new combination in *Matelea* is blocked by *M. parvifolia* (Torr.) Woodson. As *Proctor 37887* (IJ) is labelled isotype, it is assumed that the GH duplicate was intended to serve as the holotype. Dr. Proctor accompanied the current author, Dale Suiter, and Davian Campbell, on an expedition to the type locality in March of 2006. At the time the type was described the area was called Broom Hall and the valley was mostly in pineapple cultivation (Proctor, pers. comm.). On a change of ownership, the area is now mostly in coffee and under the name Baron Hall. Although the hills maintain forest cover, much is disturbed and has either been converted to coffee or is in the process of conversion. Specimens of *J. parvifolia* were not located. There are forests not owned by Baron Hall which are part of the endemic Peckham complex and may retain populations of *J. parvifolia*, but further research is needed.

Lachnostoma maritimum (Jacq.) G. Nicholson, Ill. Dict. Gard. 2:226. 1884. ≡ **Matelea maritima** (Jacq.) Woodson, Ann. Missouri Bot. Gard. 28:222. 1941.
See *Asclepias maritima* Jacq.

Lachnostoma mollis (Griseb.) M. Gómez, Anales Hist. Nat. 23:276. 1894. ≡ **Matelea mollis** (Griseb.) Woodson, Ann. Missouri Bot. Gard. 28:223. 1941.
See *Ibatia mollis* Griseb.

Macroscepis hirsuta (Vahl) Schltr. in Urban, Symb. Antill. 1:265. 1899. ≡ **Matelea hirsuta** (Vahl) Woodson in E.E. Cheesman, Fl. Trinidad 2:170. 1947.
See *Cynanchum hirsutum* Vahl.

"*Macroscepis obovata*" auct. non Kunth: Griseb., Fl. Brit. W.I. 421. 1862.
Notes: The most recent combination to which Grisebach misapplied the name *Macroscepis obovata* is *Matelea hirsuta* (Vahl) Woodson in E. E. Cheesman, Fl. Trinidad 2:170. 1947.
See *Cynanchum hirsutum* Vahl.

Marsdenia bicolor Britton & P. Wilson, Bull. Torrey Bot. Club 50:47. 1923. ≡ **Matelea bicolor** (Britton & P. Wilson) Woodson, Ann. Missouri Bot. Gard. 28:236. 1941.
Protologue: "Sierra Maestra, Oriente (*León 10787*, type; *10788*)," loc. not cited.
Type: Cuba, Oriente, Maestra ridge, 1300 m, Jul 1922, *León 10787* (HOLOTYPE: NY!; ISOTYPE: HAC, n.v.); Cuba, *León 10788* (PARATYPES: NY!, US!).
Notes: Although TROPICOS currently indicates the holotype to be at GH (as of 12 Apr 2006), the specimen is not listed in the GH online catalogue nor was it sent on loan or found in a targeted search by collection manager Emily Wood. In addition, there is a discrepancy in the label data, particularly the altitude of collection, for the paratype *Léon 10788*, suggesting that the sheets at NY and US are not duplicates of the same collection. The NY sheet indicates only "Maestra ridge, 1300 m," whereas the US sheet indicates "Woods: Sierra Maestra. Region of Pico Turquino. Alt. near 2000 m." Collector, collector number, and date are the same on both sheets.

Matelea acuminata (Griseb.) Woodson, Ann. Missouri Bot. Gard. 28:225. 1941.
See *Orthosia acuminata* Griseb.

Matelea alainii Woodson, Contr. Ocas. Mus. Hist. Nat. Colegio "De La Salle" 15:23. 1956.

Protologue: "Cuba: Oriente: on coastal limestone rocks, Km. 90 between Imías and Cajobabo, Vía Azul, Jan. 12, 1956," *Brother Alain & C.V. Morton 5029* (HT: MO); "on coastal limestone rocks. Km 50 of Via Azul, Jan 10, 1956," *Brother Alain & C.V. Morton 4959* (PT: MO).
Type: Cuba, *Alain & Morton 5029* (HOLOTYPE: MO; ISOTYPES: GH!, HAC!, US!); *Alain & Morton 4959* (PARATYPES: GH!, MO!, IJ!).

Matelea annulata Woodson ex Alain, Brittonia 20:149. 1968.
Protologue: "Hispaniola: Dominican Republic: Montiada Nueva, Barahona Prov., 21–25 Aug 1946, *R. & E. Howard 8512* (TYPE: NY; ISOTYPE: GH); Howard *8590* (GH)."
Type: Dominican Republic, Montiada Nueva, Barahona Prov., 21–25 Aug 1946, *R.A. & E.S. Howard 8512* (HOLOTYPE: NY! [2 sheets]; ISOTYPES: GH!, MO!).
Notes: Alain H. Liogier described *Matelea annulata* based on suggestions from Robert E. Woodson, Jr. and legitimized the latter's *nomen in schedula*. Three sheets were cited in the PROTOLOGUE: *R. & E. Howard 8512* (HT: NY!; IT: GH!) and *Howard 8590* (PT: GH!). The former two contain matching material. However, the latter collection (the paratype), which incidentally was also collected by both Howards, contains material that clearly does not belong to the holotype and isotype. Although also glabrous, leaves of *R. & E. Howard 8590* exhibit: (1) more numerous secondary veins, and (2) secondary veins nearly straight (vs. ascending in *R.& E. Howard 8512*). The seeds associated with *R. & E. Howard 8590* are also: (1) significantly longer (11–11.6 mm vs. 5 mm in *R. & E. Howard 8512*), (2) of a thin papery texture (vs. hardened in *R.& E. Howard 8512*), and (3) lack the distally swollen margin seen in *Howard 8512* (and other West Indian *Matelea* species). Although published as a paratype, *R. & E. Howard 8590* (GH) must be excluded from *Matelea annulata*. It remains unclear to what taxon it should be referred instead. Typification of *M. annulata* should be as indicated above. As a final note, in contrast to the indication by Liogier (1968), the flowers of *Matelea annulata* are not solitary. They appear to be borne sequentially on inflorescences subtended by a much reduced peduncle.

Matelea bayatensis (Urb.) Woodson, Ann. Missouri Bot. Gard. 28:226. 1941.
See *Gonolobus bayatensis* Urb.

Matelea bicolor (Britton & P. Wilson) Woodson, Ann. Missouri Bot. Gard. 28:236. 1941.
See *Marsdenia bicolor* Britton & P. Wilson.

Matelea borinquensis Alain, Phytologia 61:360. 1986.
Protologue: "Puerto Rico: Cerro Pelucho, San Lorenzo, alt. 400–500 m, Mar 8, 1984, *Alain & Perfa Liogier, Luis F. Martorell 35111* (holotypus: UPR)."
Type: Puerto Rico, *Liogier et al. 35111* (HOLOTYPE: UPR, n.v.).
Notes: A synonym of *Matelea variifolia* (Schltr.) Woodson fide Acevedo-Rodríguez (2005). This specimen could not be obtained on loan, despite requests.

Matelea constanzana J. Jiménez Alm., Rhodora 62:238. 1960.
Protologue: "in Sto. Domingo prope Constanza, inter frutices volubilis 1400 m. alt., *H. von Tuerckheim n. 3466*, flor. Jul. 1910," loc. not cited.
Type: The location of the type remains unknown. No additional matching material was found.
Notes: Nomen nov. for *Poicillopsis tuerckheimii* Schltr. in Urb., Symb. Antill. 7(3):339. 1912. Jiménez proposed the new name as Schlechter's epithet was unavailable in *Matelea*. The name is provisionally treated in *Matelea*, pending the rediscovery and study of the type.

Matelea correllii Spellman, Ann. Missouri Bot. Gard. 65(4):1255. 1979 ["1978"].
Protologue: "Bahama Islands. Long Island: ... low places along Queen's Highway about 4 miles north of Clarence Town center, 18 Nov. 1977, *D.S. Correll 49112* (MO, HOLOTYPE; F, FTG, GH, NY, US, ISOTYPES)."
Type: Bahamas, Long Island, *D.S. Correll 49112* (HOLOTYPE: MO; ISOTYPES: F!, FTG!, GH!, NY!, US!).

Matelea corynephora Krings, Sida 22:942. 2006.

Protologue: "Haiti. Ile la Tortue, la Vallée, top of Morne Barranca, ca. 300 m, 21 Mar 1928 (fl), *E.L. Ekman H9740* (HOLOTYPE: S!)."
Type: Haiti, Ile la Tortue, la Vallée, top of Morne Barranca, ca. 300 m, 21 Mar 1928, *E.L. Ekman H9740* (HOLOTYPE: S!).

Matelea costata (Urb.) Morillo, Anales Jard. Bot. Madrid 43:239. 1987 ["1986"].
See *Poicilla costata* Urb.

Matelea costata (Urb.) Morillo var. **goodfriendii** (Proctor) Krings, J. Bot. Res. Inst. Texas 2:150. 2008.
See *Jacaima costata* (Urb.) Rendle var. *goodfriendii* Proctor

Matelea crispiflora (Urb.) J. Jiménez Alm., Rhodora 62:238. 1960.
See *Poicillopsis crispiflora* Urb.

Matelea ekmanii (Urb.) Woodson, Ann. Missouri Bot. Gard. 28:226. 1941.
See *Gonolobus ekmanii* Urb.

Matelea denticulata (Vahl) Fontella & E.A. Schwarz, Bol. Mus. Bot. Munic. 46:4. 1981.
See *Cynanchum denticulatum* Vahl.

Matelea dictyopetala (Urb. & Ekman) Krings, J. Bot. Res. Inst. Texas 2:130. 2008.
See *Gonolobus dictyopetalus* Urb. & Ekman.

Matelea domingensis (Alain) Krings, Sida 21:2081. 2005.
See *Gonolobus domingensis* Alain.

Matelea grisebachiana (Schltr.) Alain, Mem. Soc. Cub. Hist. Nat. "Felipe Poey" 22:120. 1955.
See *Gonolobus grisebachianus* Schltr.

Matelea hastata Alain, Brittonia 20:150. 1968.
Protologue: "Haiti: Massif des Matheux, Croix des Bouquets, Morne a Cabrits, 18 Jul 1924, *Ekman H. 973* (**TYPE:** US; ISOTYPE: NY)."
Type: Haiti, *Ekman H 973* (HOLOTYPE: US!; ISOTYPES: K!, NY!)

Matelea hirsuta (Vahl) Woodson in E.E. Cheesman, Fl. Trinidad 2:170. 1947.
See *Cynanchum hirsutum* Vahl.

Matelea linearipetala Alain, Phytologia 64:346. 1988.
Protologue: "Haiti: On oligostene limestone, 200 m alt., Massif des Matheux, Thomazeau, Morne à Cabrits, Oct. 24, 1926, *E.L. Ekman 7136* (HOLOTYPUS: S)."
Type: Haiti, Morne à Cabrits, *Ekman H 7136* (HOLOTYPE: S!).

Matelea maritima (Jacq.) Woodson, Ann. Missouri Bot. Gard. 28:222. 1941.
See *Asclepias maritima* Jacq.

Matelea mollis (Griseb.) Woodson, Ann. Missouri Bot. Gard. 28:223. 1941.
See *Ibatia mollis* Griseb.

Matelea monticola Alain, Sida 20:1645. 2003.
Protologue: "Ciénaga de la Culata, Constanza, alt 1600–1700 m, 15–16 Oct 1968, *Alain Liogier 13029* (HOLOTYPE: NY; ISOTYPE: US); in woods, Cabezada de la Ciénaga de la Culata, Constanza, alt 1650 m, 16 Oct 1968, *Alain Liogier 13069* (NY, US)."
Type: Dominican Republic, Ciénaga de la Culata, Constanza, alt 1600–1700 m, 15–16 Oct 1968, *Liogier 13029* (HOLOTYPE: NY!).
Notes: A nom. nov. for *Matelea sylvicola* Alain, Phytologia 22:168. 1971, nom illeg., non L.O. Williams 1968. Neither isotype nor paratype are housed at US, despite so cited in the protologue. The paratype is also neither listed in the NY type catalogue, nor included in a loan from NY. Its location remains unknown.

Matelea nipensis (Urb.) Woodson, Ann. Missouri Bot. Gard. 28:226. 1941.
See *Gonolobus nipensis* Urb.

Matelea oblongata (Griseb.) Woodson, Ann. Missouri Bot. Gard. 28:226. 1941.
See *Orthosia oblongata* Griseb.

Matelea ovatifolia (Griseb.) Woodson, Ann. Missouri Bot. Gard. 28:225. 1941.
See *Poicilla ovatifolia* Griseb.

Matelea pauciflora (Spreng.) Woodson, Ann. Missouri Bot. Gard. 28:226. 1941.
See *Gonolobus pauciflorus* Spreng.

Matelea pentactina Krings, Sida 21:1519. 2005.
Protologue: "Haiti. Les Roseaux, Massif de la Hotte western group, rocky ledge, ca. 1300 m, 16 Sept 1928, *Ekman H 10685* (HOLOTYPE: S!); Massif de la Selle, gr. Crete-a-Piquants, Port-au-Prince, between Carrefour-Martin and Bois d'Orme, ca. 800 m, limestone, 17 Dec 1926, *Ekman H 7402* (paratype: S!)."
Type: Haiti, Les Roseaux, Massif de la Hotte western group, rocky ledge, ca. 1300 m, 16 Sept 1928, *Ekman H 10685* (HOLOTYPE: S!; ISOTYPES: B!, US!, EHH n.v.); Massif de la Selle, gr. Crete-a-Piquants, Port-au-Prince, between Carrefour-Martin and Bois d'Orme, ca. 800 m, limestone, 17 Dec 1926, *Ekman H 7402* (PARATYPE: S!, EHH n.v.).

Matelea phainops Krings, Sida 22:948. 2006.
Protologue: "Dominican Republic. Vine, up to 1.5 m high, flowers yellowish green, in thickets, about 2 mi W of Oviedo, alt. about sea level, on limestone, 3 Nov 1989 (fl), *A.H. Liogier 16617* (HOLOTYPE: GH!; ISOTYPES: NY!, USF!)."
Type: Dominican Republic, about 2 mi W of Oviedo, alt. about sea level, on limestone, 3 Nov 1989, *Liogier 16617* (HOLOTYPE: GH!; ISOTYPES: NY!, USF!).

Matelea proctori Krings, J. Bot. Res. Inst. Texas 2:151. 2008.
See *Jacaima parvifolia* Proctor

Matelea pubescens (Griseb.) Krings, J. Bot. Res. Inst. Texas 2:131. 2008.
See *Gonolobus pubescens* Griseb.

Matelea rhamnifolia (Griseb.) Krings, Sida 21:1515. 2005.
See *Gonolobus rhamnifolius* Griseb.

Matelea rhynchocephala Krings, Sida 22:949. 2006.
Protologue: "Dominican Republic. Prov. Santiago, Valle del Cibao, Santiago, Hato del Yaque, in thickets, fl. green, fruiting, 15 Feb 1930 (fl & fr), *E.L. Ekman H14296* (HOLOTYPE: S!)."
Type: Dominican Republic, Prov. Santiago, Valle del Cibao, Santiago, Hato del Yaque, in thickets, 15 Feb 1930, *E.L. Ekman H 14296* (HOLOTYPE: S!).

Matelea rubra (H. Karst.) Spellman & Morillo, Phytologia 34:152. 1976.
See *Omphalophthalma rubra* H. Karst.

Matelea rubra (H. Karst.) Aa & Stoffers, Proc. Kon. Ned. Akad. Wetensch., C 84(3):309. 1981.
Notes: *Matelea rubra* (H. Karst.) Aa & Stoffers is nomenclaturally superfluous as the combination by Spellman & Morillo (loc. cit.) has priority.
See **Matelea rubra** (H. Karst.) Spellman & Morillo.

Matelea sintenisii (Schltr.) Woodson, Ann. Missouri Bot. Gard. 28:226. 1941.
See *Gonolobus sintenisii* Schltr.

Matelea sylvicola Alain, Phytologia 22:168. 1971, nom. illeg., non L.O. Williams 1968.
See **Matelea monticola** Alain.

Matelea tamnifolia (Griseb.) Woodson, Ann. Missouri Bot. Gard. 28:225. 1941.
See *Poicilla tamnifolia* Griseb.

Matelea tigrina (Griseb.) Woodson, Ann. Missouri Bot. Gard. 28:226. 1941.
See *Gonolobus tigrinus* Griseb.

Matelea torulosa Krings, Sida 22:951. 2006.
Protologue: "Dominican Republic. Distr. Nacional, Los 3 Ojos de Agua, near Santo Domingo, 31 Oct 1959 (fl), *E. Marcano [J.J. Jiménez] 4096* (HOLOTYPE: US!)."
Type: Dominican Republic, Distr. Nacional, Los 3 Ojos de Agua, near Santo Domingo, 31 Oct 1959, *E. Marcano [J.J. Jiménez] 4096* (HOLOTYPE: US!).

Matelea variifolia (Schltr.) Woodson, Ann. Missouri Bot. Gard. 28:226. 1941.
See *Gonolobus variifolius* Schltr.

Matelea viridiflora (G. Mey.) Woodson, Ann. Missouri Bot. Gard. 28:325. 1941.
See *Cynanchum denticulatum* Vahl (syn. fide Howard 1989b).

Matelea viridivenia Alain, Phytologia 22:169. 1971.
Protologue: "Cabo Rojo, Pedernales, 4 Nov 1969, Alain Liogier 16637 (HOLOTYPE, NY; ISOTYPES: US, GH, P, IJ); about 5 miles E of Cabo Rojo, 8 Feb 1969, Alain Liogier 13620 fruiting specimen (NY); in thickets, km 92 from Bani to Azua, alt 80 m, 3 Nov 1969, Alain Liogier 16598 (NY, US, GH, P); on limestone, los Guanitos, 7 mi E of Cabo Rojo, Pedernales, 13 Nov 1969, Alain Liogier 16961b (NY, US, GH, P, IJ)."
Type: Dominican Republic, Cabo Rojo, Pedernales, 4 Nov 1969, *Alain Liogier 16637* (HOLOTYPE: NY!); about 5 miles E of Cabo Rojo, 8 Feb 1969, *Alain Liogier 13620* fruiting specimen (paratype: NY!); in thickets, km 92 from Bani to Azua, alt 80 m, 3 Nov 1969, *Alain Liogier 16598* (paratype: NY!); on limestone, los Guanitos, 7 mi E of Cabo Rojo, Pedernales, 13 Nov 1969, *Alain Liogier 16961b* (paratype: NY!, USF!).
Notes: The types or paratypes listed in the protologue for GH, IJ, P, and US have not been found.

Omphalophthalma rubra H. Karst., Fl. Columb. 2:119, t. 163. 1866. ≡ **Matelea rubra** (H. Karst.) Spellman & Morillo, Phytologia 34:152. 1976.
Protologue: "Habitat litora maris Caribaei prope St. Martam [Colombia], "loc. not cited.
Type: Colombia [New Granada], St. Marta, Herb. Karsten (HOLOTYPE: LE [Sennikov, pers. comm.; n.v., not sent on loan due to budget constraints]).

Orthosia acuminata Griseb., Cat. Pl. Cub. 175. 1866. ≡ **Matelea acuminata** (Griseb.) Woodson, Ann. Missouri Bot. Gard. 28:225. 1941.
Protologue: "Cuba or. (*Wr. 2966*)," loc. not cited.
Type: Cuba, Oriente, *Wright 2966*, 1860–1864 (LECTOTYPE designated by Krings & Fantz 2006: GH!; ISOLECTOTYPES: BM!, G!, HAC! [2 sheets], K!).
Notes: Krings and Fantz (2006) noted that sheets of *Wright 2966* (BM, G, GH, HAC, and K) bear white labels with the dates 1860–64. The mounted field ticket on the GH sheet reads: "Asclepias – Fl. (except the white stigma) green. Farallones San Andre Oct 27." As *Wright 2966* (GH!) contains fifteen inflorescences and is in very good condition; it was designated as lectotype for *Orthosia acuminata* Griseb. by Krings and Fantz (2006). *Wright 2966* (G!) contains four inflorescences and is in superior condition to the HAC material. *Wright 2966* (BM!, G!, HAC!, K!) should be considered isolectotypes. See Krings and Fantz 2006 for additional discussion regarding their philosophy of typification of Wright specimens.

Orthosia oblongata Griseb., Cat. Pl. Cub. 176. 1866. ≡ **Matelea oblongata** (Griseb.) Woodson, Ann. Missouri Bot. Gard. 28:226. 1941.
Protologue: "Cuba occ. (*Wr. 2967*)," loc. not cited.
Type: Cuba, *Wright 2967*, 1860–1864 (LECTOTYPE designated by Krings & Fantz 2006: GH!; ISOLECTOTYPES: BM!, G!, HAC!, K!, MO, S!).
Notes: Krings and Fantz (2006) noted that sheets of the original material for *O. oblongata*—at BM!, G!, GH!,

HAC!, K!, MO, and S!—all bear white labels with the dates 1860–64. The mounted field ticket of *Wright 2967* (GH) reads: "Asclepias – Fl. green – a white speck at the tips of the segments. Stigma white. Loma de Ranjel June 17." Field tickets do not accompany the other specimens. Krings and Fantz (2006) designated *Wright 2967* (GH) lectotype for *Orthosia oblongata* Griseb., considering the duplicates at G, HAC, K, MO. and S isolectotypes. *Wright 2967* (GH) is in good condition, with numerous inflorescences. See Krings and Fantz (2006) for additional discussion regarding their philosophy of typification of Wright specimens.

Poicilla acuminata (Griseb.) Schltr. in Urban, Symb. Antill. 5(3):469. 1908. ≡ **Matelea acuminata** (Griseb.) Woodson, Ann. Missouri Bot. Gard. 28:225. 1941.
See *Orthosia acuminata* Griseb.

Poicilla costata Urb., Symb. Antill. 6(1):38. 1909. ≡ **Matelea costata** (Urb.) Morillo, Anales Jard. Bot. Madrid 43:239. 1987 ["1986"].
Protologue: "Hab. in Jamaica juxta viam ad Wareka in Long Mountain ad latus australe, 200 m. alt., m. Nov. fl., m. Jun. fruct.: Harris n. 9590, 10006," loc. not cited.
Type: Jamaica, road to Wareka, Long Mountain, S side, 19 Nov 1907 (fl), *W. Harris 10006* (LECTOTYPE, here designated: BM!; ISOLECTOTYPE: UCWI!); Jamaica, Long Mountain, S side, 600 feet altitude, 21 Jun 1907 (fr), *W. Harris 9590* (SYNTYPES: NY!; UCWI!).
Notes: *Harris 9590* (NY) is annotated in Urban's hand.

Poicilla mollis (Griseb.) Schltr. in Urban, Symb. Antill. 5(3):470. 1908. ≡ **Matelea mollis** (Griseb.) Woodson, Ann. Missouri Bot. Gard. 28:223. 1941.
See *Ibatia mollis* Griseb.

Poicilla oblongata (Griseb.) Schltr. in Urban, Symb. Antill. 5(3):470. 1908. ≡ **Matelea oblongata** (Griseb.) Woodson, Ann. Missouri Bot. Gard. 28:226. 1941.
See *Orthosia oblongata* Griseb.

Poicilla ovatifolia Griseb., Cat. Pl. Cub. 177. 1866. ≡ **Matelea ovatifolia** (Griseb.) Woodson, Ann. Missouri Bot. Gard. 28:225. 1941.
Protologue: "Cuba or. (*Wr. 2965*)," loc. not cited.
Type: Cuba, Oriente, *Wright 2965* (LECTOTYPE designated by Krings and Fantz 2006: GOET!; SYNTYPES: BM!; BREM!, G!, GH!, HAC!, K n.v., LE n.v., NY!, P!, S!, UC!).
Notes: As Krings and Fantz (2006) noted, no field tickets accompany the GOET specimen or any syntype, except the GH specimen. Accompanying field tickets of the GH specimen suggest that the sheet is comprised of at least two collections made at different times (Mar, Jun), although three fragments are mounted. The two fragments mounted on the right contain inflorescences; the fragment mounted on the left contains infructescences. Both field tickets refer to flowers with neither one mentioning fruits. Fruits are not described in Grisebach's protologue and are not present on any other syntype beside the GH specimen. Except for the GOET specimen, collection labels of all other known specimens are white and bear the dates 1860–64. The GOET specimen bears a tan label with a printed date of 1860, although the zero appears to have been crossed out. It is heavily written on in Grisebach's hand and is herein designated lectotype for *Poicilla ovatifolia* Griseb. The studied (and matching) duplicately-numbered material in other herbaria remain syntypes.

Poicilla tamnifolia Griseb., Cat. Pl. Cub. 176. 1866. ≡ **Matelea tamnifolia** (Griseb.) Woodson, Ann. Missouri Bot. Gard. 28:225. 1941.
Protologue: "Cuba or., in monte Toro pr. Potosi (*Wr.*)," loc. not cited.
Type: Cuba, San José, 5 Oct, *Wright s.n.* (LECTOTYPE, here designated: GH!); *Wright s.n.* (SYNTYPE: NY! [fragment]).
Notes: See discussion under *Gonolobus tigrinus* regarding problems of typification of Grisebach names based on Wright collections. Unfortunately, there is no extant Wright material corresponding to *Poicilla tamnifolia* at GOET. However, a specimen does exist at GH, which can be designated lectotype following Howard (1989a): Cuba, San José, 5 Oct, *Wright s.n.*

Poicillopsis crispiflora Urb., Feddes Repert. 19:7. 1923. ≡ **Matelea crispiflora** (Urb.) Jiménez, Rhodora 62:238. 1960.
Protologue: "Haiti prope Furcy 1500 m alt., m. Sept. flor.: *Buch no. 1995*," loc. not cited.
Type: Haiti, prope Furcy, im Gebüsch, Blth weiss, 1500 m alt., m. Sept. flor., *Buch no. 1995* (LECTOTYPE, here designated: IJ!).
Notes: *Buch 1995* consists of four flowers in two umbellate inflorescences and a few leaves on stems, though most are in a fragment pocket. The single additional collection of this species that matches the protologue is *Ekman H1933* (EHH n.v., K!, S!): Haiti, Morne de la Selle, Furcy, 1540m, in Buchs [sic] Botan. Garden, 17 Sept 1924. The sheets at K and S are in exceedingly good condition, bearing numerous leaves and flowers. The sheet at EHH has not been seen, but is listed here based on the catalogue provided by: http://www.umce.ca/cours/martin/herbier_ekman/recherche.pl.

Poicillopsis ovatifolia (Griseb.) Schltr. in Urban, Symb. Antill. 7(3):339. 1912. ≡ **Matelea ovatifolia** (Griseb.) Woodson, Ann. Missouri Bot. Gard. 28:225. 1941.
See *Poicilla ovatifolia* Griseb.

Poicillopsis tuerckheimii Schltr. in Urban, Symb. Antill. 7(3):339. 1912.
See **Matelea constanzana** J. Jiménez Alm.

Ptycanthera berterii Decne. in de Candolle, Prodr. 8:606. 1844, nom. illeg.
Protologue: "S. Domingo (*Bertero*) [...] (v.s.h. DC.)."
Type: Hispaniola, 'St. Domingue,' *Bertero s.n.* (HOLOTYPE: G-DC [IDC microfiche Candolle Prodromus Herbarium, fiche # 1543!]; ISOTYPE: P!).
Notes: The name *Ptycanthera berterii* Decne. is illegitimate as the nomenclatural type is the same as that of *Gonolobus pauciflorus* Spreng. (see above). Schlechter (1899) misapplied Decaisne's name to *Orthosia acuminata* Griseb. (syn. *Matelea acuminata* (Griseb.) Woodson).

Ptycanthera mollis (Griseb.) Schltr. in Urban, Symb. Antill. 1(2):280. 1899. ≡ **Matelea mollis** (Griseb.) Woodson, Ann. Missouri Bot. Gard. 28:223. 1941.
See *Ibatia mollis* Griseb.

Ptycanthera oblongata (Griseb.) Schltr. in Urban, Symb. Antill. 1(2):280. 1899. ≡ **Matelea oblongata** (Griseb.) Woodson, Ann. Missouri Bot. Gard. 28:226. 1941.
See *Orthosia oblongata* Griseb.

Ptycanthera ovatifolia (Griseb.) Schltr. in Urban, Symb. Antill. 1(2):279. 1899. ≡ **Matelea ovatifolia** (Griseb.) Woodson, Ann. Missouri Bot. Gard. 28:225. 1941.
See *Poicilla ovatifolia* Griseb.

Vincetoxicum acuminatum (Griseb.) M. Gómez, Anales Acad. Ci. Med. Habana 23:276. 1894. ≡ **Matelea acuminata** (Griseb.) Woodson, Ann. Missouri Bot. Gard. 28:225. 1941.
See *Orthosia acuminata* Griseb.

Vincetoxicum oblongatum (Griseb.) M. Gómez, Anales Acad. Ci. Med. Habana 23:276. 1894. ≡ **Matelea oblongata** (Griseb.) Woodson, Ann. Missouri Bot. Gard. 28:226. 1941.
See *Orthosia oblongata* Griseb.

Vincetoxicum sintenisii (Schltr.) Britton in Britton & P. Wilson, Sci. Surv. Porto Rico & Virgin Islands 6:100. 1925. ≡ **Matelea sintenisii** (Schltr.) Woodson, Ann. Missouri Bot. Gard. 28:226. 1941.
See *Gonolobus sintenisii* Schltr.

Vincetoxicum stephanotrichum (Griseb.) Britton in Britton & P. Wilson, Sci. Surv. Porto Rico & Virgin Islands 6:100. 1925.
See **Gonolobus stephanotrichus** Griseb.

Vincetoxicum variifolia (Schltr.) Britton in Britton & P. Wilson, Sci. Surv. Porto Rico & Virgin Islands 6:100. 1925. ≡ **Matelea variifolia** (Schltr.) Woodson, Ann. Missouri Bot. Gard. 28:226. 1941.
See *Gonolobus variifolius* Schltr.

Names of uncertain application or excluded from Gonolobinae. The following names include those for which neither protologues nor types could be obtained, or for which the specimens do not belong in Gonolobinae. Names of the former category have long been placed in synonymy by authors of treatments of West Indian Gonolobinae (e.g., Schlechter 1899; Alain 1957).

Cynanchum crispiflorum Sw., Prodr. 52. 1788. ≡ *Fischeria crispiflora* (Sw.) K. Schum., Nat. Pflanzenfam. 4(2):230. 1895.
Protologue: "India Occidentalis, Jamaica," loc. not cited.
Type: Plum., Pl. amer. 216, f. 1. 1759.
Notes: According to Murphy (1986), the name *Cynanchum crispiflorum* Sw. (and various subsequent combinations in *Fischeria*) has been misapplied by various workers to what she recognized as *Fischeria scandens* DC. Murphy (1986) excluded the type of *C. crispiflorum* Sw. from *Fischeria* and recognized only the following two species in the West Indies: *F. scandens* DC. (Cuba and Jamaica) and *F. stellata* (Vell.) Fourn. (Trinidad). A current annotation in TROPICOS suggests that the type of *C. crispiflora* Sw.—the Plumier figure—may be *Prestonia agglutinata* (Jacq.) Woodson (≡ *Allotoonia agglutinata* (Jacq.) J.F. Morales & J.K. Williams). I am unfamiliar with this latter taxon, but a comparison of the Plumier figure to that of *Allotoonia agglutinata* (syn. *Echites agglutinata*) as illustrated in Acevedo-Rodríguez (2005), shows differences in the corolla lobes (linear-lanceolate in Acevedo-Rodríguez (2005) vs. suborbicular in the Plumier figure).

Fischeria crispiflora (Sw.) Schltr. in Urban, Symb. Antill. 1(2):268. 1899, nom. illeg.
Notes: A superfluous combination; see *F. crispiflora* (Sw.) K. Schum.

Fischeria crispiflora (Sw.) K. Schum., Nat. Pflanzenfam. 4(2):230. 1895.
See *Cynanchum crispiflorum* Sw.

Gonolobus crispiflorus (Sw.) R.Br. ex Schult., Syst. Veg. 6:60. 1820.
See *Cynanchum crispiflorum* Sw.

Gonolobus ottonis C. Koch & Bouche, Ind. Sem. Hort. Berol. 13. 1855.
Protologue: unknown.
Type: unknown.
Notes: Sometimes cited as *Gonolobus ottonis* Walp. (Ann. Bot. Syst. 5:502. 1859.). However, Walpers (1859) clearly cited *G. ottonis* C. Koch & Bouche and should not be considered author of a homonym. Walpers (1859) repeated Koch and Bouche's citation: 'Ex insula Cuba reportavit *Otto*.' However, Schlechter (1899) thought that the specimen collected by Otto (apparently formerly at B) was from Caracas, Venezuela, not from Cuba. The location of the type is unknown.

Gonolobus oxyanthus Turcz., Bull. Soc. Imp. Naturalistes Moscou 25(2):318. 1852.
Protologue: "Venezuela, Funck 2," fide TROPICOS (protologue n.v.).
Type: Venezuela, 1845–1852, Funk 2 (G, n.v.; P, n.v.) fide TROPICOS.
Notes: Fide Fontella & Schwarz (1981), a synonym of *Gonolobus rostratus* (Vahl) R.Br. ex Schult. (*Systema Vegetabilium* 6:61. 1820). TROPICOS (23 Aug 2006) cited *Funk* 2 (Venezuela) as the type, but a copy of the protologue could not be located. Specimens were not found on either of two visits to P.

Gonolobus virescens Desv. ex Ham., Prodr. Pl. Ind. Occid. 32. 1825.
Protologue: "Herb. Prof. Desvaux, Jamaica. (S. v.)," loc. not cited.
Type: "Jamaica," Herb. Desvaux (HOLOTYPE: P!).
Notes: Rendle (1936) considered *G. virescens* Desv. a *species incerta*. Schlechter (1899) noted that there was likely a locality mix-up between *G. stapelioides* and *G. virescens*, and that the latter was likely collected from

Tobago and not Jamaica (see discussion under *G. stapelioides* above). The morphology of the flowers of *Desvaux s.n.* (P) places it in Marsdenieae Benth., rather than Gonolobinae.

Lachnostoma ovatum Turcz., Bull. Soc. Imp. Naturalistes Moscou 25(2):318. 1852.
Protologue: unknown.
Type: unknown.
Notes: Cited as *L. ovata* and as a synonym for *Matelea ovatifolia* (Griseb.) Woodson by Alain (1957). Neither protologue, nor type could be located.

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BOOK REVIEWS

ELISEO "CHEO" TORRES AND TIMOTHY L. SAWYER, JR. 2005. **Curandero: A Life in Mexican Folk Healing.** (ISBN 0-8263-3640-x, pbk.). University of New Mexico Press, 1312 Basehart Rd. SE, Albuquerque, New Mexico 87106-4363, U.S.A. (**Orders:** www.unmpress.com, 1-800-249-7737). $14.95, 170 pp., b/w illustrations, 5 1/2" × 8".

I first became interested in herbal medicine while listening to my mother's stories about our foremothers' skillful use of medicinal plants. These grandmothers and the local curanderos were the main sources of medical care for families living on the remote ranches of South Texas and Northern Mexico. The personalized stories in Dr. Torres's book resonate with the common culture of Southwestern Mexican-American traditional folk medicine, or curanderismo. Chapter 10 "How I Was Fed and Healed by Plants" is an account of the herbal wisdom of Dr. Torres's mother that brought back many memories. Dr. Torres's mother grew medicinal plants in old coffee cans that were handed out freely to sick friends and family, as did my own grandmother. Through my mother I was already familiar with one of the legendary healers profiled in this book, Don Pedrito Jaramillo, a folk saint whose tombstone near Falfurrias, Texas, reads "The Benefactor of Humanity."

Reading *Curandero* has been both a pleasure and an education. Although it is not intended to be a scientific ethnobotanical text, this book does much to promote cultural literacy and understanding of a beloved folk medicine system that exists in various forms throughout the Southwestern United States. Curanderismo incorporates elements of European and Arabic medicine brought over from the Old World with elements of Native American traditional medicine. The personalized stories about the practitioners of curanderismo, the curanderos, allow the reader to understand this form of folk medicine from within the culture. Dr. Torres is an expert who teaches summer courses on curanderismo at the University of New Mexico. This book would make useful reading for anyone interested in herbal and folk medicine, as well as for researchers and healthcare professionals interested in learning more about a form of traditional medicine that incorporates spirituality and the mind with healing.—*Marissa N. Oppel, MS, Coordinator, Science Learning Laboratories, Biology Department, El Centro College, Dallas, Texas 75202, U.S.A.*

L. KATHERINE KIRKMAN, CLAUD L. BROWN, AND DONALD J. LEOPOLD. 2007. **Native Trees of the Southeast: An Identification Guide.** (ISBN 13: 978-0-88192-828-0, pbk.). Timber Press, Inc., 133 S.W. Second Avenue, Suite 450, Portland, Oregon 97204-3527, U.S.A. (**Orders:** www.timberpress.com, orders@timberpress.com, 1-800-827-5622). $34.95, 370 pp., numerous drawings, maps, images, keys, 6.25" × 9.25".

Contents.—Preface; Acknowledgments; Introduction; Categories of plant classification; Scientific and common names; How to use the keys; Identification features of trees; Tree diversity of southeastern forests; Summer keys to trees; Winter keys to flowering trees; [Descriptions of 44 plant families]; Some common introduced and naturalized trees in the Southeast; Glossary; Conversion tables; Bibliography; Index.

This book, *Native Trees of the Southeast: An Identification Guide*, is divided into sections by family. The authors include a detailed introduction that provides the reader with their specific definition of a tree and information on how to use keys and features to identify trees. The authors' use of line drawings helps to clearly explain the diversity of tree anatomy, specifically concerning leaves and branches. A winter and summer key were included and will aide the reader in identifying any species during any season of the year.

I found this book to be very informative and a good source for any amateur or avid outdoorsman. The authors used both common and scientific names in their description of each species. They provide a simple ruler on the back cover of the book to aide in field measurements for identification to species. The inclusion of a winter and summer key was a great addition. The authors used easy to understand terms in each key for defining the specific parts of a tree. I found the images and maps to be very useful, except I would suggest that at least one image or line drawing be included for each species. The book's size and weight make it an ideal companion for any hiker or outdoorsman.—*Keri McNew, MS Biology, Project Manager, Botanical Research Institute of Texas, 500 East 4th Street, Fort Worth, Texas 76102-4025, U.S.A.*

MOLECULAR PHYLOGENETIC ANALYSIS OF THE AMERICAN STIPEAE (POACEAE) RESOLVES *JARAVA* SENSU LATO POLYPHYLETIC: EVIDENCE FOR A NEW GENUS, *PAPPOSTIPA*

Konstantyn Romaschenko

M.G. Kholodny
Institute of Botany
National Academy of Sciences of Ukraine
01601 Kiev, UKRAINE
kromaschenko@gmail.com

Paul M. Peterson and Robert J. Soreng

Department of Botany
National Museum of Natural History
Smithsonian Institution
Washington, DC 20013-7012, U.S.A.
peterson@si.edu; sorengr@si.edu

Nuria Garcia-Jacas

Laboratory of Molecular Analysis
Botanic Institute of Barcelona (CSIC-ICUB)
Pg. del Migdia, s. n.
08038 Barcelona, SPAIN
ngarciajacas@ibb.csic.es

Oksana Futorna

M.G. Kholodny Institute of Botany
National Academy of Sciences of Ukraine
01601 Kiev, UKRAINE
oksana_drofa@yahoo.com

Alfonso Susanna

Botanic Institute of Barcelona (CSIC-ICUB)
Pg. del Migdia, s. n.
08038 Barcelona, SPAIN
asusanna@ibb.csic.es

ABSTRACT

A molecular phylogenetic analysis based on plastid (*trn*K-*mat*K, *mat*K, *trn*H-*psb*A, and *trn*L-*trn*F regions) and nuclear ITS DNA sequences of 68 species representing 11 genera suggests an entirely new hypothesis for the evolutionary history within the tribe. *Piptochaetium*, *Anatherostipa*, *Ptilagrostis* and *Hesperostipa* are basal lineages that diverge independently from a clade that includes a monophyletic *Jarava* subg. *Pappostipa* (rendering *Jarava* s.l. polyphyletic) that is sister group to *Austrostipa* plus a subclade referred to as the "Major American Clade" (MAC). Within the MAC, New World *Achnatherum* is the sister group of a grade or clade of *Jarava* s.s. and a *Nassella*-*Amelichloa* clade. *Jarava* subg. *Pappostipa* is monophyletic and not closely related to other sampled species of *Jarava*, supporting recognition of the new genus **Pappostipa** (Speg.) Romaschenko, P.M. Peterson & Soreng with 23 species; *Stipa speciosa* selected as the lectotype. Within *Pappostipa* we identify two clades that we recognize as new sections, and we make new combinations to transfer *Jarava* subsp. *Pappostipa* species to the new genus: *Pappostipa* sect. **Chrysovaginatae** Romaschenko, with the following new combinations: **Pappostipa sorianoi** (Parodi) Romaschenko, **Pappostipa atacamensis** (Parodi) Romaschenko, **Pappostipa nana** (Speg.) Romaschenko, **Pappostipa ibarii** (Phil.) Romaschenko, **Pappostipa ibarii** f. **pallescens** (Parodi) Romaschenko, **Pappostipa ibarii** var. **anomala** (Parodi) Romaschenko, **Pappostipa ameghinoi** (Speg.) Romaschenko, **Pappostipa ameghinoi** var. **digona** (Parodi) Romaschenko, **Pappostipa ameghinoi** var. **precordillerana** (F.A. Roig) Romaschenko, **Pappostipa chubutensis** (Speg.) Romaschenko, **Pappostipa chubutensis** var. **hirsutissima** (F.A. Roig) Romaschenko, **Pappostipa frigida** (Phil.) Romaschenko, **Pappostipa frigida** var. **parvispicula** (Parodi) Romaschenko, **Pappostipa humilis** (Cav.) Romaschenko, **Pappostipa humilis** var. **decrescens** (Kuntze) Romaschenko, **Pappostipa humilis** var. **ruiziana** (Parodi) Romaschenko, **Pappostipa chrysophylla** (E. Desv.) Romaschenko, **Pappostipa chrysophylla** f. **minuta** (F.A. Roig) Romaschenko, **Pappostipa chrysophylla** var. **cordillerarum** (Parodi) Romaschenko, **Pappostipa chrysophylla** var. **crispula** (Kuntze) Romaschenko, and **Pappostipa chrysophylla** f. **modica** (F.A. Roig) Romaschenko. *Pappostipa* sect. **Pappostipa** includes the following new combinations: **Pappostipa speciosa** (Trin. & Rupr.) Romaschenko, **Pappostipa speciosa** var. **manqueclensis** (F.A. Roig) Romaschenko, **Pappostipa speciosa** var. **atuelensis** (F.A. Roig) Romaschenko, **Pappostipa speciosa** var. **parva** (F.A. Roig) Romaschenko, **Pappostipa speciosa** var. **breviglumis** (Parodi) Romaschenko, **Pappostipa speciosa** var. **ciliata** (F.A. Roig) Romaschenko, **Pappostipa speciosa** f. **horrida** (F.A. Roig) Romaschenko, **Pappostipa speciosa** f. **abscondita** (F.A. Roig) Romaschenko, **Pappostipa speciosa** var. **media** (Torres) Romaschenko, **Pappostipa vaginata** (Phil.) Romaschenko, **Pappostipa vaginata** f. **rigida** (F.A. Roig) Romaschenko, **Pappostipa vaginata** f. **inmersa** (F.A. Roig) Romaschenko, **Pappostipa vaginata** f. **laevis** (F.A. Roig) Romaschenko, **Pappostipa vaginata** f. **contracta** (F.A. Roig) Romaschenko, **Pappostipa vaginata** var. **argyroidea** (F.A. Roig) Romaschenko, **Pappostipa vaginata** var. **dilatata** (F.A. Roig) Romaschenko, **Pappostipa nicorae** (F.A. Roig) Romaschenko, **Pappostipa hieronymusii** (Pilg.) Romaschenko, **Pappostipa patagonica** (Speg.) Romaschenko, **Pappostipa maeviae** (F.A. Roig) Romaschenko,

Pappostipa parodiana (F.A. Roig) Romaschenko, **Pappostipa braun-blanquetii** (F.A. Roig) Romaschenko, **Pappostipa semperiana** (F.A. Roig) Romaschenko, **Pappostipa ruiz-lealii** (F.A. Roig) Romaschenko, **Pappostipa malalhuensis** (F.A. Roig) Romaschenko, **Pappostipa major** (Speg.) Romaschenko, **Pappostipa vatroensis** (F.A. Roig) Romaschenko, and **Pappostipa barrancaensis** (F.A. Roig) Romaschenko.

RESUMEN

Un análisis filogenético basado en los datos moleculares de varías regiones plastidiales (*trn*K-*mat*K, *mat*K, *trn*H-*psb*A y *trn*L-*trn*F), y las secuencias nucleares del ITS de 68 especies representando 11 géneros, resulta en una nueva hipótesis de la historia evolutiva de la tribu. El conjunto de los *Piptochaetium*, *Anatherostipa*, y *Ptilagrostis* (con *Hesperostipa* como un clado adyacente) se presenta como un linaje basal que diverge independientemente del clado monofiletico que incluye *Jarava* subg. *Pappostipa* (lo que hace *Jarava* s.l. polifilético) que es, a su vez, un grupo hermano para *Austrostipa* y un subclado al que nos como "clado americano mayor" (MAC). Dentro del MAC el *Achnatherum* del Nuevo Mundo se presenta como un grupo hermano para un complejo formado por los clados de *Jarava* s.s. y *Nassella* con el género *Amelichloa* incloido. El hecho de que *Jarava* subg. *Pappostipa* sea monofiletico y no se relacione con el resto del *Jarava* s.l. apoya la separación del *Pappostipa* (Speg.) Romaschenko, P.M. Peterson & Soreng como un genero nuevo con 23 especies; *Stipa speciosa* seleccionado como el lectotipo. Dentro del *Pappostipa* las dos secciones fueron reconocidas basando sobre los datos moleculares y morfológicos. Para la transferencia del *Jarava* subsp. *Pappostipa* a un género nuevo se proponen las necesarias combinaciones taxonómicas apropiadas: *Pappostipa* secc. **Chrysovaginatae** Romaschenko, con las siguientes combinaciones nuevas: **Pappostipa sorianoi** (Parodi) Romaschenko, **Pappostipa atacamensis** (Parodi) Romaschenko, **Pappostipa nana** (Speg.) Romaschenko, **Pappostipa ibarii** (Phil.) Romaschenko, **Pappostipa ibarii** f. **pallescens** (Parodi) Romaschenko, **Pappostipa ibarii** var. **anomala** (Parodi) Romaschenko, **Pappostipa ameghinoi** (Speg.) Romaschenko, **Pappostipa ameghinoi** var. **digona** (Parodi) Romaschenko, **Pappostipa ameghinoi** var. **precordillerana** (F.A. Roig) Romaschenko, **Pappostipa chubutensis** (Speg.) Romaschenko, **Pappostipa chubutensis** var. **hirsutissima** (F.A. Roig) Romaschenko, **Pappostipa frigida** (Phil.) Romaschenko, **Pappostipa frigida** var. **parvispicula** (Parodi) Romaschenko, **Pappostipa humilis** (Cav.) Romaschenko, **Pappostipa humilis** var. **decrescens** (Kuntze) Romaschenko, **Pappostipa humilis** var. **ruiziana** (Parodi) Romaschenko, **Pappostipa chrysophylla** (E. Desv.) Romaschenko, **Pappostipa chrysophylla** f. **minuta** (F.A. Roig) Romaschenko, **Pappostipa chrysophylla** var. **cordillerarum** (Parodi) Romaschenko, **Pappostipa chrysophylla** var. **crispula** (Kuntze) Romaschenko, and **Pappostipa chrysophylla** f. **modica** (F.A. Roig) Romaschenko. Dentrode *Pappostipa* secc. **Pappostipa** proponemos las nuevas combinaciones siguientes: **Pappostipa speciosa** (Trin. & Rupr.) Romaschenko, **Pappostipa speciosa** var. **manqueclensis** (F.A. Roig) Romaschenko, **Pappostipa speciosa** var. **atuelensis** (F.A. Roig) Romaschenko, **Pappostipa speciosa** var. **parva** (F.A. Roig) Romaschenko, **Pappostipa speciosa** var. **breviglumis** (Parodi) Romaschenko, **Pappostipa speciosa** var. **ciliata** (F.A. Roig) Romaschenko, **Pappostipa speciosa** f. **horrida** (F.A. Roig) Romaschenko, **Pappostipa speciosa** f. **abscondita** (F.A. Roig) Romaschenko, **Pappostipa speciosa** var. **media** (Torres) Romaschenko, **Pappostipa vaginata** (Phil.) Romaschenko, **Pappostipa vaginata** f. **rigida** (F.A. Roig) Romaschenko, **Pappostipa vaginata** f. **inmersa** (F.A. Roig) Romaschenko, **Pappostipa vaginata** f. **laevis** (F.A. Roig) Romaschenko, **Pappostipa vaginata** f. **contracta** (F.A. Roig) Romaschenko, **Pappostipa vaginata** var. **argyroidea** (F.A. Roig) Romaschenko, **Pappostipa vaginata** var. **dilatata** (F.A. Roig) Romaschenko, **Pappostipa nicorae** (F.A. Roig) Romaschenko, **Pappostipa hieronymusii** (Pilg.) Romaschenko, **Pappostipa patagonica** (Speg.) Romaschenko, **Pappostipa maeviae** (F.A. Roig) Romaschenko, **Pappostipa parodiana** (F.A. Roig) Romaschenko, **Pappostipa braun-blanquetii** (F.A. Roig) Romaschenko, **Pappostipa semperiana** (F.A. Roig) Romaschenko, **Pappostipa ruiz-lealii** (F.A. Roig) Romaschenko, **Pappostipa malalhuensis** (F.A. Roig) Romaschenko, **Pappostipa major** (Speg.) Romaschenko, **Pappostipa vatroensis** (F.A. Roig) Romaschenko y **Pappostipa barrancaensis** (F.A. Roig) Romaschenko.

The tribe Stipeae Dumort. are temperate, cool-season (C_3) grasses that generally occupy somewhat moist to predominantly dry open grasslands and steppe communities in all continents except Antarctica. Worldwide the Stipeae consist of a minimum of 21 genera and 524–604 species, depending on how Asian taxa are recognized (Soreng & Davis 2005). In the New World there are 279 species of Stipeae (Soreng et al. 2008); of these, 222 (79.6%) are found in South America. Thirteen genera are indigenous, and nine are endemic to the New World. The Stipeae s.s. (excluding elements of Phaenospermateae Renvoize & Clayton, and subtribes Ampelodesminae Connert and Duthieinae Pilg. ex Potztal) are characterized by having single-flowered spikelets with terminally-awned lemmas where the awn is the result of the fusion between the central and two lateral vascular traces, simple starch grains, florets with two or three linear lodicules, and small-sized chromosomes with a base number of x = 10–12. The Stipeae are placed in subfamily Pooideae (GPWG 2001). Within the Pooideae they are an 'early diverging' lineage that arose after the separations of the Brachyelytreae Ohwi, and Lygeeae J. Presl plus Nardeae W.D.J. Koch (Davis & Soreng 2007).

Historically, delimitation of genera within the American Stipeae was based on a broad concept of the genus *Stipa* L. Hitchcock (1935, 1951) accepted three genera in North America: *Oryzopsis* Michx., *Piptochaetium* J. Presl, and *Stipa*. In South American Stipeae, Spegazzini (1901) recognized only *Aciachne* Benth.,

Oryzopsis, and *Stipa*. In the second part of the 20th century, Stipeae taxonomy was characterized by the consecutive resurrection of previously described genera or emendation of taxa considered by Spegazzini (1901, 1925) as subgenera of *Stipa*. *Nassella* (Trin.) E. Desv. was restored to generic status by Parodi (1947) and significantly expanded, and thus became the most species rich genus among American Stipeae (Barkworth 1990; Barkworth & Torres 2001). In considering the distribution of morphological features among stipoid grasses and lemma epidermal features (Thomasson 1978, 1980, 1981, 1982), Barkworth and Everett (1987) suggested that *Stipa* includes only Eurasian species: Hence the name *Stipa* should not be used for any American species. In subsequent major rearrangements of the American Stipeae, five species were transferred to *Hesperostipa* (M.K. Elias) Barkworth. Thirty-seven other American species formerly placed in *Stipa* or *Oryzopsis* were shown to share some morphological features with the Eurasian representatives of *Achnatherum* P. Beauv.; they were transferred to the latter genus (Barkworth 1993). *Stipa* subg. *Anatherostipa* Hack. ex Kuntze (Kuntze 1898; Spegazzini 1901, 1925), including the Obtusae group of Parodi (1946), was recently established at the generic rank by Peñailillo (1996), currently with 11 species (Soreng et al. 2003). *Nassella* now includes 115 and *Piptochaetium* 35 species, respectively (Soreng et al. 2003).

The genus *Jarava* Ruiz et Pav. was resurrected by Rojas (1997), in the sense of *Stipa* subg. *Jarava* (Ruiz et Pav.) Trin. & Rupr. (Caro & Sánchez 1973), and significantly expanded by Peñailillo (2002, 2003) to 55 species by inclusion of *Stipa* subg. *Pappostipa* Speg. and *S.* subg. *Ptilostipa*. Speg. The expansion of *Jarava* effectively completed the removal of all remaining accepted indigenous New World species from the genus *Stipa*, as anticipated by Barkworth and Everett (1987). However, Stipeae taxonomists generally acknowledged that such a broadly circumscribed *Jarava* was probably polyphyletic, and Arriaga and Barkworth (2006) began to revise it by transferring five *Jarava* s.l. species to a new genus, *Amelichloa* Arriaga & Barkworth.

Parodi (1960) recognized two main morphological leaf types in Spegazzini's *Stipa* subg. *Pappostipa*, represented by *Stipa speciosa* and *S. humilis* (Arriaga 1983). The first type (leaf anatomical "type I" of Arriaga 1983) encompassed species with stiff, thick, and usually pungent leaves. The second type ("type II" of Arriaga 1983) covered species with comparatively thin, slender, and non-pungent leaves. Later, Parodi (1960), followed by Roig (1964) and Nicora and Rúgolo de Agrasar (1978), noted that species with the former type had brownish-red basal sheaths and species with the latter type had pale basal sheaths.

There have been several attempts to infer phylogenetic relationships among stipoid genera based on morphological evidence (Tzvelev 1977; Barkworth & Everett 1987; Thomasson 1978, 1985) and preliminary molecular analyses (Jacobs et al. 2000, 2007; Cialdella et al. 2007). The origins of *Hesperostipa*, *Jarava* s.s., *Piptochaetium*, and *Stipa* s.s. have been reported as monophyletic (Jacobs et al. 2000, 2007; Cialdella et al. 2007), but the overall phylogeny of the American Stipeae remains poorly resolved and contradictory.

Our preliminary study of the Stipeae phylogeny based on ITS sequence data (Romaschenko et al. 2007) revealed a deep separation between a Euro-Mediterranean clade, including *Stipa* s.s., and a clade including genera and species of East Asian, Australian, and American origin. In addition, *Jarava* (sensu Peñailillo 2003) was resolved as polyphyletic, with a clade of species formerly placed in *Stipa* subg. *Pappostippa*, clearly independently derived from the core species of *Jarava* s.s.

The main objectives of this paper are to present a phylogenetic hypothesis for the American Stipeae and to evaluate the monophyly of *Jarava* s.l. based on an analyses of plastid (*mat*K, *trn*K-*mat*K, *trn*H-*psb*A and *trn*L-*trn*F) and nuclear ribosomal ITS DNA sequences. We also discuss morphological and anatomical characters that support our phylogenetic inferences.

METHODS

Taxon sampling.—The majority of the specimens sampled in this study were collected by PMP and RJS, and are deposited at the Smithsonian Institution, United States National Herbarium (US). Eighty-one samples representing 66 species and three infraspecific taxa, with duplicates for nine taxa, were included in our analysis (Table 1). These represent eight of the 11 Stipeae genera reported as indigenous for the Americas (Soreng et al. 2003), plus the newer segregate genus, *Amelichloa*. Thirteen species collectively of minor South

Table 1. Stipeae species sampled, sources of material, vouchers, and GenBank accession numbers for DNA sequences. Species with an asterisk* now in *Pappostipa*; sequence partially incomplete with a degree ° symbol; [1,2,3] = duplicate specimens sampled.

Taxon	Country	Voucher	trnK-matK	matK	trnH-psbA	trnL-trnF	ITS
Achnatherum aridum (M.E. Jones) Barkworth	USA	*Tiehm & Nachlinger 13518* (US)	EU489382	EU489170	EU489237	EU489311	EU489089
Achnatherum occidentale (Thurb. ex. S. Watson) Barkworth	Canada	*Saarela, Sears & Maze 594* (UBC)	EU489383	EU489171	EU489238	EU489312	EU489090
Achnatherum occidentale subsp. *pubescens* (Vasey) Barkworth	USA	*Soreng 7418* (US)	EU489384	EU489172	EU489239	EU489313	EU489091
Achnatherum parishii (Vasey) Barkworth	USA	*Roos & Roos 4895* (US)	EU489385	–	EU489240	EU489314	EU489092
Achnatherum richardsonii (Link) Barkworth	Canada	*Peterson, Saarela & Smith 18399* (US)	EU489386	EU489173	–	EU489315	EU489093
Amelichloa caudata (Trin.) Arriaga & Barkworth[1]	Argentina	*Pyke 596* (BC)	EU489387	EU489174	–	EU489316	EU489094
Amelichloa caudata (Trin.) Arriaga & Barkworth[2]	Argentina	*Peterson & Annable 11398* (US)	EU489388	EU489175	EU489241	EU489317	EU489095
Amelichloa clandestina (Hack.) Arriaga & Barkworth	Mexico	*Hoge, Barkworth & Carranza 286* (US)	EU489389	–	EU489242	–	EU489096°
Anatherostipa bomanii (Hauman) Peñailillo	Bolivia	*Peterson, Soreng & Romaschenko 20710* (US)	EU489390	EU489176	EU489243	EU489318	EU489097
Anatherostipa hans-meyeri (Pilg.) Peñailillo	Peru	*Peterson, Soreng & Romaschenko 20645* (US)	EU489391	EU489177	EU489244	EU489319	EU489098
Anatherostipa rigidiseta (Pilg.) Peñailillo	Peru	*Peterson, Soreng & Romaschenko 20724* (US)	EU489392	EU489178	EU489245	EU489320	EU489099
Austrostipa compressa (R.Brown) S.W.L. Jacobs & J. Everett	Australia	*Peterson, Soreng & Rosenberg 14514* (US)	EU489393	EU489179	EU489246	EU489321	EU489100
Austrostipa pycnostachya (Benth.) S.W.L. Jacobs & J. Everett	Australia	*Peterson, Soreng & Rosenberg 14318* (US)	EU489394	EU489180	EU489247	EU489322	EU489101
Austrostipa scabra (Lindl.) S.W.L. Jacobs & J. Everett	Australia	*Peterson, Soreng & Rosenberg 14442* (US)	EU489395	EU489181	EU489248	EU489323	EU489102
Austrostipa scabra subsp. *falcata* (Hughes) S.W.L. Jacobs & J. Everett	Australia	*Blaylock 1496* (KW)	EU489396	EU489182	EU489249	EU489324	EU489103
Austrostipa tenuifolia (Steudel) S.W.L. Jacobs & J. Everett	Australia	*Peterson, Soreng & Macfarlane 14248* (US)	EU489397	EU489183	EU489250	EU489325	EU489104
Brachyelytrum erectum (Schreb.) P. Beauv.	USA	*Soreng 7440* (US)	EU489398	EU489184	EU489251	EU489326	EU489105

Taxon	Country	Voucher	trnK-matK	matK	trnH-psbA	trnL-trnF	ITS
Hesperostipa comata (Trin. & Rupr.) Barkworth ssp. *comata*	Canada	*Saarela, Sears & Maze 595* (UBC)	EU489399	EU489185	EU489252	EU489327	EU489106
Hesperostipa neomexicana (Thurb.) Barkworth	Mexico	*Peterson & Valdes-Reyna 18934* (US)	EU489400	EU489186	–	EU489328	EU489107
Hesperostipa spartea (Trin.) Barkworth	USA	*Holmes 214* (US)	EU489401	EU489187	EU489253	EU489329	EU489108
**Jarava atacamensis* (Parodi) Peñailillo[1]	Chile	*Peterson, Soreng, Finot & Judziewicz 15447* (US)	EU489402	EU489188	EU489254	EU489330	EU489109
**Jarava atacamensis* (Parodi) Peñailillo[2]	Chile	*Peterson, Soreng & Judziewicz 15480* (US)	EU489403	EU489189	–	EU489331	EU489110
**Jarava barrancaensis* (F.A. Roig) Peñailillo	Argentina	*Peterson & Annable 11371* (US)	EU489404	EU489190	EU489255	EU489332	EU489111
Jarava castellanosii (F.A. Roig) Peñailillo	Argentina	*Peterson & Annable 10336* (US)	EU489405	EU489191	EU489256	EU489333	EU489112
**Jarava chrysophylla* (E. Desv.) Peñailillo[1]	Argentina	*Peterson & Annable 11466* (US)	EU489406	EU489192	EU489257	EU489334	EU489113
**Jarava chrysophylla* (E. Desv.) Peñailillo[2]	Argentina	*Peterson, Soreng, Salariato & Panizza 19220* (US)	EU489407	EU489193	EU489258	EU489335	EU489114
**Jarava chrysophylla* (E. Desv.) Peñailillo[3]	Argentina	*Peterson, Soreng, Salariato & Panizza 19297* (US)	EU489408	EU489194	EU489259	EU489336	EU489115
**Jarava frigida* (Phil.) F. Rojas[1]	Argentina	*Peterson, Soreng, Salariato & Panizza 19360* (US)	EU489409	EU489195	EU489260	EU489337	EU489116
**Jarava frigida* (Phil.) F. Rojas[2]	Argentina	*Peterson & Annable 10397* (US)	–	EU489196	EU489261	EU489338	EU489117
**Jarava hieronymusii* (Pilg.) Peñailillo	Argentina	*Peterson & Annable 11488* (US)	EU489410	EU489197	EU489262	EU489339	EU489118
**Jarava humilis* (Cav.) Peñailillo[1]	Argentina	*Peterson & Annable 11258* (US)	EU489411	EU489198	EU489263	EU489340	EU489119
**Jarava humilis* (Cav.) Peñailillo[2]	Argentina	*Peterson & Annable 11317* (US)	EU489412	EU489199	EU489264	EU489341	EU489120
**Jarava humilis* (Cav.) Peñailillo[3]	Argentina	*Peterson, Soreng, Salariato & Panizza 19169* (US)	EU489413	EU489200	EU489265	EU489342	EU489121
Jarava hystricina (Speg.) Peñailillo	Argentina	*Peterson, Soreng, Salariato & Panizza 19550* (US)	–	–	–	–	EU489122
**Jarava ibarii* (Phil.) Peñailillo	Chile	*Soreng 7331* (US)	EU489414	EU489201	EU489266	EU489343	EU489123
Jarava ichu Ruiz & Pav.[1]	Peru	*Peterson, Soreng & Romaschenko 20745* (US)	EU489415	EU489202	EU489267	EU489344	EU489124
Jarava ichu Ruiz & Pav.[2]	Peru	*Peterson, Soreng & Romaschenko 20270* (US)	EU489416	EU489203	EU489268	EU489345	EU489125
Jarava juncoides (Speg.) Peñailillo	Argentina	*Ruiz Leal & Paci 465* (US)	EU489417	–	EU489269°	–	EU489126°
Jarava leptostachya (Griseb.) F. Rojas[1]	Argentina	*Peterson & Annable 11714* (US)	EU489418	EU489204	EU489270	EU489346	EU489127
Stipa leptostachya var. *capilliseta* (Hitchc.) Parodi[2]	Bolivia	*Villavicencio & Sukopp 52* (US)	–	–	EU489271	–	EU489128
Jarava media (Speg.) Peñailillo	Argentina	*Peterson, Soreng, Salariato & Panizza 19337* (US)	EU489419	EU489205	EU489272	EU489347	EU489129
**Jarava nicorae* (F.A. Roig) Peñailillo	Argentina	*Peterson & Annable 11408* (US)	EU489420	EU489206	EU489273	EU489348	EU489130
**Jarava patagonica* (Speg.) Peñailillo	Argentina	*Senn 4292* (US)	–	–	–	–	EU489131

Taxon	Country	Voucher	trnK-matK	matK	trnH-psbA	trnL-trnF	ITS
Jarava plumosa (Spreng.) S.W.L. Jacobs & J. Everett	Argentina	*Schinini, Vanni, Arbo, Horni & Aranda 29135* (US)	EU489421	–	EU489274°	EU489349	EU489132
Jarava plumosula (Nees ex Steud.) F. Rojas	Peru	*Peterson, Soreng & Romaschenko 20471* (US)	EU489422	EU489207	EU489275	EU489350	EU489133°
Jarava polyclada (Hack.) Peñailillo	Argentina	*Peterson & Annable 11569* (US)	EU489423	EU489208	EU489276	EU489351	EU489134°
Jarava pseudoichu (Caro) F. Rojas	Peru	*Peterson, Soreng & Romaschenko 20736* (US)	EU489424	EU489209	EU489277	EU489352	EU489135
Jarava scabrifolia (Torres) Peñailillo	Argentina	*Peterson & Annable 11712* (US)	EU489425	EU489210	EU489278	EU489353	EU489136
**Jarava speciosa* (Trin. & Rupr.) Peñailillo	Argentina	*Peterson & Annable 11549* (US)	EU489426	EU489211	EU489279	EU489354	EU489137
**Jarava speciosa* var. *major* (Speg.) Peñailillo[1]	Chile	*Soreng 7222* (US)	EU489427	EU489212	EU489280	EU489355	EU489138
**Jarava speciosa* var. *major* (Speg.) Peñailillo[2]	Argentina	*Peterson & Annable 11292* (US)	EU489428	EU489213	EU489281	EU489356	EU489139
**Jarava speciosa* var. *major* (Speg.) Peñailillo[3]	Argentina	*Peterson, Soreng, Salariato & Panizza 19216* (US)	EU489429	EU489214	EU489282	EU489357	EU489140
**Jarava vaginata* (Phil.) F. Rojas[1]	Argentina	*Peterson, Soreng, Salariato & Panizza 19222* (US)	EU489430	EU489215	EU489283	EU489358	EU489141
**Jarava vaginata* (Phil.) F. Rojas[2]	Argentina	*Peterson & Annable 11744* (US)	EU489431	EU489216	EU489284	EU489359	EU489142
Nardus stricta L.	Kyrgyzstan	*Soreng 7497* (US)	EU489432	EU489217	EU489285	EU489360	EU489143
Nassella brachychaetoides (Speg.) Barkworth	Bolivia	*Peterson & Annable 11748* (US)	EU489433	EU489218	EU489286	EU489361	EU489144
Nassella brachyphylla (Hitchc.) Barkworth	Bolivia	*Peterson, Soreng & Romaschenko 20631* (US)	EU489434	EU489219	EU489287	EU489362	EU489145
Nassella caespitosa Griseb.	Argentina	*Peterson, Soreng, Salariato & Panizza 19540* (US)	EU489435	EU489220	EU489288	EU489363	EU489146
Nassella clarazii (Ball) Barkworth	Argentina	*Peterson & Annable 11651* (US)	EU489436	EU489221	EU489289	EU489364	EU489147
Nassella dasycarpa (Hitchc.) Torres	Argentina	*Peterson & Annable 10344* (US)	EU489437	EU489222	EU489290	EU489365	EU489148
Nassella depauperata (Pilg.) Barkworth	Peru	*Cano et al. 13740* (USM)	EU489438	EU489223	EU489291	EU489366	EU489149
Nassella filiculmis (Delile) Barkworth	Chile	*Soreng 7009* (US)	EU489439	EU489224	EU489292	EU489367	EU489150
Nassella inconspicua (J. Presl) Barkworth	Bolivia	*Renvoize 5333* (US)	EU489440	–	EU489293	EU489368	EU489151
Nassella manicata (E. Desv.) Barkworth	Chile	*Soreng 7000* (US)	EU489441	EU489225	EU489294	–	EU489152°
Nassella meyeniana (Trin. & Rupr.) Parodi	Argentina	*Peterson & Annable 10301* (US)	EU489442	EU489226	EU489295	EU489369	EU489153°
Nassella nardoides (Phil.) Barkworth	Argentina	*Peterson & Annable 11773* (US)	EU489443	EU489227	EU489296	EU489370	EU489154°
Nassella neesiana (Trin. & Rupr.) Barkworth	Argentina	*Peterson & Annable 10258* (US)	EU489444	EU489228	EU489297	EU489371	EU489155
Nassella nidulans (Mez) Barkworth	Argentina	*Seijo 1871* (US)	EU489445	–	EU489298	–	EU489156°

Taxon	Country	Voucher	trnK-matK	matK	trnH-psbA	trnL-trnF	ITS
Nassella pfisteri (Matthei) Barkworth	Chile	*Soreng 7017a* (US)	EU489446	EU489229	EU489299	EU489372	EU489157
Nassella pubiflora (Trin. & Rupr.) E. Desv.	Argentina	*Peterson & Annable 11618* (US)	EU489447	EU489230	EU489300	EU489373	EU489158
Nassella rosengurttii (Chase) Barkworth	Uruguay	*Rosengurtt 216* (US-Type)	EU489448	–	EU489301	–	EU489159
Nassella rupestris (Phil.) Torres	Argentina	*Peterson & Annable 10347* (US)	EU489449	–	EU489302	EU489374	EU489160
Nassella sanluisensis (Speg.) Barkworth	Argentina	*Roig 3293* (US)	–	–	EU489303	EU489375	EU489161
Nassella sellowiana (Nees ex Trin. & Rupr.) Peñailillo	Brazil	*Reitz & Klein* 5314 (US)	–	–	EU489304	–	EU489162
Nassella tenuissima (Trin.) Barkworth	Argentina	*Pyke 992* (BC)	EU489450	EU489231	–	–	EU489163
Nassella trichotoma (Nees) Hack. ex Arechav.	Argentina	*Peterson & Annable 11506* (US)	EU489451	EU489232	EU489305	EU489376	EU489164
Piptochaetium brachyspermum (Speg.) Parodi	Argentina	*Peterson & Annable 11252* (US)	EU489452	EU489233	EU489306	EU489377	EU489165
Piptochaetium panicoides (Lam.) E. Desv.	Chile	*Soreng 7011* (US)	EU489453	EU489234	EU489307	EU489378	EU489166
Piptochaetium ruprechtianum E. Desv.	Argentina	*Peterson & Annable 11401* (US)	EU489454	EU489235	EU489308	EU489379	EU489167
Ptilagrostis mongholica (Turcz. ex Trin.) Griseb.	Kazakhstan	*Goloskokov s.n.* (LE)	EU489455	–	EU489309	EU489380	EU489168
Ptilagrostis porteri (Rydb.) W.A. Weber	USA	*Cooper* 1940 (US)	EU489456	EU489236	EU489310	EU489381	EU489169

American genera (*Aciachne*, *Lorenzochloa* Reeder & C. Reeder, *Ortachne* Nees ex Steud.), the North American genus *Oryzopsis* s.s., and North American species placed in *Piptatherum* (all other species are Old World), are not included in the present analysis because our preliminary data indicate that they have no effect on the disposition of taxa of concern here. One Asian species of *Ptilagrostis* Griseb. and five Australian species of *Austrostipa* S.W.L. Jacobs & J. Everett were included to show evidence of the geographical heterogeneity among some phylogenetic branches. Subsequent papers will include a much larger sample among the Stipeae. *Brachyelytrum erectum* and *Nardus stricta* were chosen as outgroups based on the results of recent analyses of phylogenetic relationships in *Pooideae* (Hilu et al. 1999; Soreng & Davis 2000; GPWG 2001; Davis & Soreng 2007; Soreng et al. 2007). These outgroups were used to root trees in the ITS analyses of the Stipeae (Jacobs et al. 2000; Romaschenko et al. 2007).

DNA extraction, amplification, and sequencing.—Leaf tissue was homogenized using Qiagen TissueLyser, and DNA was isolated using a BioSprint 96 DNA Plant Kit (Qiagen, Valencia, California, USA, 2005). For some specimens, the CTAB method (Doyle & Doyle 1987) was used.

PCR amplifications were performed in MJ Research or PE 9700 thermal cyclers. Genomic DNA was combined with 1x reaction buffer (200 mM Tris-HCl, 500 mM NH_4) (Bioline Biolase Taunton, Madison, USA) without Mg++, 2 mM $MgCl_2$, 200 mM dNTP's, 1.5μl of Taq polymerase (Bioline Biolase Taunton, Madison, USA), 40 pmol/μl each of forward and reverse primers.

The entire nuclear ribosomal ITS region was amplified using primers ITS1, ITS2, ITS3, ITS4, ITS5 (White et al. 1990) and ITS5A (Stanford et al. 2000) with the following thermal cycler settings: initial denaturation step of 2 min at 94°C, followed 35 cycles at 94°C for 30 s, 50–55°C for 30 s, 72°C for 1 min 30 s, and a final extension of 10 min at 72°C.

Four chloroplast DNA regions were sequenced: *trn*K-*mat*K, *mat*K, *trn*H^{GUG}-*psb*A, and *trn*L5'-*trn*F. The 5'-end of *trn*K-*mat*K and 5'- *mat*K were amplified separately. The 5'*trn*K-*mat*K readily amplified using the forward primer *trn*K3914F (Johnson & Soltis 1995) and newly designed reverse primer *trn*K660SR (5'-CGAATGATGATACATAGTGC-3') positioned close to the end of the 5'-*trn*K-*mat*K intron. The reverse complement (i.e. forward version) of the latter primer (*trn*K660SF; 5'-GCACTATGTATCATCATTCG-3') and the reverse complement of a slightly modified *mat*K1412F primer (Johnson & Soltis 1995; i.e., *mat*K1412SR 5'- CTGATACATAAGAGTTRTAT-3') were used to amplify ~555 pb of the 5'-end of *mat*K. The *trn*H^{GUG}-*psb*A intergenic spacer was amplified with primers *trn*H^{GUG} (Tate & Simpson 2003) and *psb*A (Sang et al. 1997). The *trn*L-*trn*F region (which included a portion of 3'-*trn*L intron, the 3'-*trn*L exon, and the *trn*L-*trn*F intergenic spacer) was amplified using primers 5'*trn*L^{UAA}(f) and *trn*F^{GAA}(c) [Taberlet et al. 1991]. The amplification parameters for all chloroplast regions were: 94°C, 2 min; 35 cycles of 94°C for 45 s, 58–62°C for 45 s, 72°C for 1 min 30 s; 72°C for 10 min. PCR products were cleaned with ExoSAP-IT (USB, Cleveland, Ohio, USA). DNA sequencing was performed with BigDye Terminator Cycle Sequencing v.3.1 (PE Applied Biosystems, Foster City, CA, USA) according to the following parameters: 80°C, 5 min; 25 or 30 cycles of 95°C for 10 s, 50°C for 5 s and 60°C for 4 min. Sequenced products were analyzed on an ABI PRISM 3730 DNA Analyzer 7900HT (ABI).

Sequences were aligned manually using BioEdit v.7.0.5.3 (Hall 1999) and then by eye. All sequences were submitted to GenBank (http://www.ncbi.nlm.nih.gov); voucher information, and GenBank accession numbers are provided in Table 1. Even though some indels, especially in chloroplast regions, seemed to be very specific for phylogenetic groups, they were not re-coded for this analysis and were excluded along with ambiguously aligned regions. The following gene regions were excluded: *trn*K-*mat*K with four regions of 2–25 bp in length; *trn*H-*psb*A with 10 regions of 1–4 (–22) bp in length; *trn*L-*trn*F with 31 regions from 1–6 (–20) bp; and ITS with 15 regions 1–4 (–22) bp. No regions were excluded from *mat*K. All gaps were treated as missing data. Parsimony analysis was performed using PAUP v. 4.0b10 (Swofford 2000) and PAUPRat v.1b (Sikes & Lewis 2001), which implements the Parsimony Ratchet of Nixon (1999). Parsimony searches were carried out for individual regions, combined plastid, and combined plastid and nuclear regions. In searching for the optimal tree, the heuristic method was implemented and tree bisection-reconnection (TBR)

was chosen as a branch swapping algorithm. Character states were specified as unordered and unweighted. PAUPRat searches were set for generating 1001 most parsimonious trees. Because PAUPRat finds the most parsimonious tree in each iteration, a set of 1001 iterations is recommended by program developers as sufficient to derive a consensus tree. All of the most parsimonious trees in our analyses were of the same length. These data sets were used to yield the majority-rule consensus trees.

Bayesian posterior probabilities were estimated using MrBayes v.3.01 (Huelsenbeck & Ronquist 2001; Ronquist et al. 2005) and the best-available substitution model was selected using MrModeltest 1.1b (Nylander 2002). The symmetrical model (SYM+I+G; Zharkikh 1994) with gamma-distributed rate variation across sites was selected by hierarchical likelihood ratio tests (hLRT) and Akaike information criterion. Bayesian analysis was initiated with random starting trees and was initially run for 1×10^6 generations with sampling frequency of the chains set to every 100th iteration. If this number of generations was not sufficient for the Markov chains to reach stasis, additional generations were invoked. The standard deviation value of the split frequencies below 0.01 indicates that Markov chains reached their stasis (Ronquist et al. 2005). The number of generations needed to complete the analysis varied from 1×10^6 for individual DNA regions to 4×10^6 in analysis of the combined data. Branches with posterior probabilities (PP) >0.95 were considered statistically significant. For additional information about the stability of phylogenetic groups the branch frequency or parsimony frequency (BF) value was used. The BF value indicates how often a branch appeared in the analysis, i.e., when this value was 100% it means the node appeared unchanged in all iterations (i.e., strict consensus).

Bootstrap has a long history of being used as a standard measure when estimating phylogeny and we have included bootstrap analysis. Felsenstein (1985) states, "Bootstrapping provides us with a confidence interval within which is contained not the true phylogeny, but the phylogeny that would be estimated on repeated sampling of many characters from the underlying pool of characters." We agree with Felsenstein that bootstrap values are measures of repeatability rather than measures of accuracy (see Soltis & Soltis 2003). Regardless of interpretation, bootstrap values are affected by the number of characters supporting the clade of interest and the data set as a whole (Soltis & Soltis 2003). For a dataset with no conflict among characters, at least three characters are needed to provide 95% support (Felsenstein 1985). With real data a greater number of characters may be needed to achieve 95% support (Soltis & Soltis 2003). Thus bootstrap tends to be overly conservative, often underestimating a well-supported clade (Sanderson & Wojciechowski 2000). Bootstrap (BS) values were calculated using PAUP v. 4.0b10 (Swofford 2000) from 10×10^6 fast-heuristic bootstrap replicates with random addition sequence. Sequence divergence was calculated based on the uncorrected "p" distance measure included in Neighbor-joining search settings.

Scanning electron microscopy.—Lemma ultra structure was studied using dry mature seeds sampled from herbarium of the following species used in the phylogenetic analysis: *Jarava chrysophylla*, *Jarava speciosa*, *Jarava nicorae*, *Jarava pseudoichu*, *Jarava plumosula*, and *Amelichloa caudata*. Wax from the seed surface was removed by soaking the seeds in xylol solution for six to eight hours. After soaking, seeds were mounted on scanning electron microscopy sample tables. Mounted samples were covered with gold in the vacuum spray gun (JII-4X, Japan). The ultra structure of the lemma was studied using scanning electron microscope Jeol (JSM35C, Japan) at varying magnifications.

Light microscopy.—Cross-sections of leaf blades were prepared with the use of a rotary microtome. Intact leaf blades of *Jarava barrancaensis*, *Jarava speciosa* var. *major*, and *Jarava chrysophylla* from herbarium specimens were rehydrated for 10–12 min in distilled water at 100 °C. For studies of the sclerenchyma tissue, the cross-sections were stained with safranin.

RESULTS

Amplification of the *trn*K intron was significantly improved when the 5'-end of the intron and the maturase K gene were amplified separately. This enabled us to optimize our protocol for routine amplification of all chloroplast regions, even when old herbarium material was used. With this approach, PCR reactions were

up to 60% more successful than when the traditional intron primers were used (i.e., *trn*K3914F-2R). Consequently, the *trn*K[1] intron had the highest rate of amplification (92.6%) compared to the non-coding regions *trn*H-*psb*A (91.4%) and *trn*L-*trn*F (89%), which are traditionally considered to be the most easily amplified regions of the chloroplast genome (e.g., Kress et al. 2005). The *mat*K gene had a lower rate of amplification (85.2%); lack of *mat*K sequence data for a subset of taxa probably affected branch support in the combined chloroplast analysis. For the most of the silica preserved samples or recently collected herbarium specimens the entire ITS region was easily amplified (100%). A few specimens that lack several chloroplast regions were not included in the chloroplast analysis but we did include them in the combined analysis based on ITS and partial plastid sequences. A small subset of samples with two or more missing chloroplast regions was included in the combined analysis (see Table 1 for details). The plastid data set is missing 11.4% and the combined analysis is missing 9%, mostly due to unsequenced plastid regions for some samples. There is no missing ITS data.

Analyses of DNA sequences.—The general characteristics of the DNA regions used to infer phylogeny in our data set are detailed in Table 2. The greatest number of potentially parsimony informative characters per region was provided by the nuclear DNA ITS region.

The topologies of the trees produced by parsimony and Bayesian analyses for each of the four plastid regions sequenced were not inconsistent with that produced by the combined plastid data. Since the separate plastid datasets had comparatively low numbers of parsimony informative characters and low levels of sequence divergence they were combined (Fig. 1). The phylogenetic signals of the intergenic spacer *trn*H–*psb*A and *trn*L–*trn*F region were stronger than other gene regions and were slightly better resolved, partly due to their higher level of sequence divergence (Table 2).

No conspicuous differences between topologies derived from the *trn*H–*psb*A and *trn*L–*trn*F regions were found in this analysis. The only region that had informative substitutions responsible for separation of the *Pappostipa* clade of *Jarava* s.l. was the *trn*L–*trn*F region (data not shown).

The ITS tree was more than two times longer than the plastid tree and had lower CI and RI values (Table 2). There was relatively minor topological incongruence among clades in the trees generated from the combined plastid DNA-ITS data set (Fig. 3) and the ITS data (Fig. 2).

The monophyly of the Stipeae is well supported (BF=100, PP=0.64–1.00, BS=96–100) in all three cladograms (Figs. 1–3). Several major clades were consistently resolved in all three analyses (Fig. 1–3). A clade including *Achnatherum, Amelichloa, Austrostipa, Jarava* s.l., and *Nassella* [AAAJN] was detected in all three analyses (Figs. 1–3). Within the AAAJN clade a primary deep split between the *Pappostipa* clade and the clade of *Austrostipa* plus *Achnatherum, Jarava* (excluding the *Pappostipa* clade), *Nassella* and *Amelichloa* was maintained in all three analyses (Figs. 1–3). *Austrostipa* (from Australia) was resolved in all three analyses as sister to a clade of *Achnatherum, Jarava* (excluding the *Pappostipa* clade), *Nassella,* and *Amelichloa*; this relationship received strong support only in the nuclear and combined analyses. The latter clade is denoted in Figs. 1–3 as the Major American Clade or **MAC**.

Within MAC, *Achantherum* was always monophyletic and the sister group of the rest of the clade. A clade of *Nassella* with *Amelichloa* nested within it was detected in all three analyses (Figs. 1–3); this clade and always excluded elements of *Jarava*.

Table 2 summary statistics show the highest rate of parsimony informative characters, ingroup–outgroup and ingroup sequence divergence for nuclear rDNA ITS region. Analysis of the combined plastid-ITS data set (Fig. 3) showed deep splits among the American stipoids, also detected by the separate analyses, and separation of the *Pappostipa* clade. The Stipeae genera included in this analysis were resolved as monophyletic groups with three exceptions. *Ptilagrostis* resolved in a polytomy in the plastid analysis, but the species were united in the ITS and combined analyses. *Jarava* s.l. was divided into a *Pappostipa* clade and a *Jarava* s.s. (*Jarava* excluding the *Pappostipa* clade) clade (Fig. 3), or grade (Figs. 1&2). *Jarava* s.s. was resolved as a paraphyletic grade to *Nassella* (encompassing *Amelichloa*) in the independent plastid and ITS analyses, but the species were united in the combined analysis. Additionally, as detected in the separate plastid and ITS

TABLE 2. Summary of *trnK-matK*, *matK*, *trnH-psbA*, *trnL-trnF*, and ITS regions used in this study.

	trnK-matK	***matK***	***trnH-psbA***	***trnL-trnF***	**Combined plastid data**	**ITS**	**Combined plastid & nuclear data**
Sequence bp length (range)	571–556	555	585–567	612–541	2315–2231	592–584	2904–2271
Number of taxa	75	69	74	72	75	81	81
Number of characters	588	555	663	686	2537	640	3177
Number of informative characters	24	22	23	33	97	137	222
Ingroup-outgroup divergence (%)	3.62	4.22	5.2	7.35	–	14.34	–
Ingroup divergence (%)	0.79	0.78	0.87	0.84	–	4.31	–
Tree length	33	31	37	56	155	380	519
Consistency index (CI)	0.85	0.77	0.73	0.68	0.72	0.50	0.55
Retention index (RI)	0.98	0.95	0.96	0.93	0.95	0.82	0.87
Homoplasy index (HI)	0.15	0.22	0.27	0.32	0.27	0.50	0.44
Rescaled consistency index (RC)	0.83	0.74	0.70	0.63	0.68	0.40	0.48

analyses, *Nassella* was only resolved as monophyletic if *Amelichloa* is subsumed within it. Goodness-of-fit statistics i.e., consistency index, retention index, and rescaled consistency index, for the combined plastid DNA-nrDNA set was higher than for nrDNA set alone.

Early diverging clades at the base of the Stipeae included the genera *Ptilagrostis* (only as a polytomy in Fig. 1), *Anatherostipa*, and *Piptochaetium*. All analyses supported these genera as independent lineages at the current level of taxon sampling (Figs. 1–3). Resolution of relationships among these three genera varied among the datasets. Analysis of the plastid data set yielded a consensus topology with these genera and *Hesperostipa* in a polytomy with a large clade including *Jarava* s.l., *Austrostipa*, *Achnatherum*, *Nassella*, and *Amelichloa* [**AAAJN**]. Analysis of the ITS data set yielded a stepwise grade leading to *Hesperostipa* as sister group to AAAJN. The analysis of the combined plastid-nuclear data set resulted in a fully resolved and a moderately well supported resolved basal clade of *Ptilagrostis* as sister group to *Anatherostipa* and *Piptochaetium* (Fig. 3; BF=71, PP=0.93), and *Hesperostipa* as sister group to AAAJN (Fig. 3; BF=100, PP=1.00, BS=100). Henceforth, for ease of discussion, we call the set of *Anatherostipa*, *Piptochaetium* and *Ptilagrostis* the "***basal lineages***" (BL in Figs. 1–3). The position of these the basal lineages with respect to the core of the tree needs further examination, particularly including Old World genera, and is not the focus of the present study. Both of the *Piptochaetium* groups (Cialdella et al. 2007), *Piptochaetium* sect. *Podopogon* (Raf.) Parodi (*P. ruprechtianum*) and *Piptochaetium* sect. *Piptochaetium* (*P. panicoides*) are represented in the analysis. In all topologies, the *Piptochaetium* clade had high statistical support (BF=100, PP=0.95–1.00, BS=59–96; Figs. 1–3).

Representatives of the two extant geographical lineages of *Ptilagrostis* chosen for analysis were *P. mongholica* from Asia and *P. porteri* from the Americas. These species formed a consistent and well supported clade (BF=100, PP=1.00, BS=95) on the ITS tree (Fig. 2) and the combined tree (Fig. 3; BF=100, PP=1.00, BS=97). A phylogenetic relationship between these two species was resolved as a polytomy in the consensus tree from the plastid analysis (Fig. 1).

There are two clades adjacent to the basal lineages. One comprises the representatives of the genus *Hesperostipa* in a clade in all three trees (BF=100, PP=0.99–1.00, BS=99–100; Figs. 1–3). A second clade contains AAAJN members showing deep split (polyphyly) in the genus *Jarava*: *Stipa* subg. *Pappostipa* (*Pappostipa* clade) of Spegazzini (1901) elements of *Jarava* are separated from *Jarava* s.s. by sequentially diverging clades of *Austrostipa* and *Achnatherum* (BF=99–100; PP=0.63, <0.50, 0.99; BS=99, <50, 99; respectively in Figs. 1–3). In combined analyses as well as separate nuclear DNA ITS sequence analysis, the *Pappostipa* clade was well supported (BF=100, PP=0.95–1.00, BS=69–99; Figs. 2 & 3).

In all analyses, the Australian *Austrostipa* clade was sister group to MAC. These clades had high statistical support (BF=100; PP=0.68–1.00; BS=90, <50, 80; respectively in Figs. 1–3) and their relationship as sister clades was consistent.

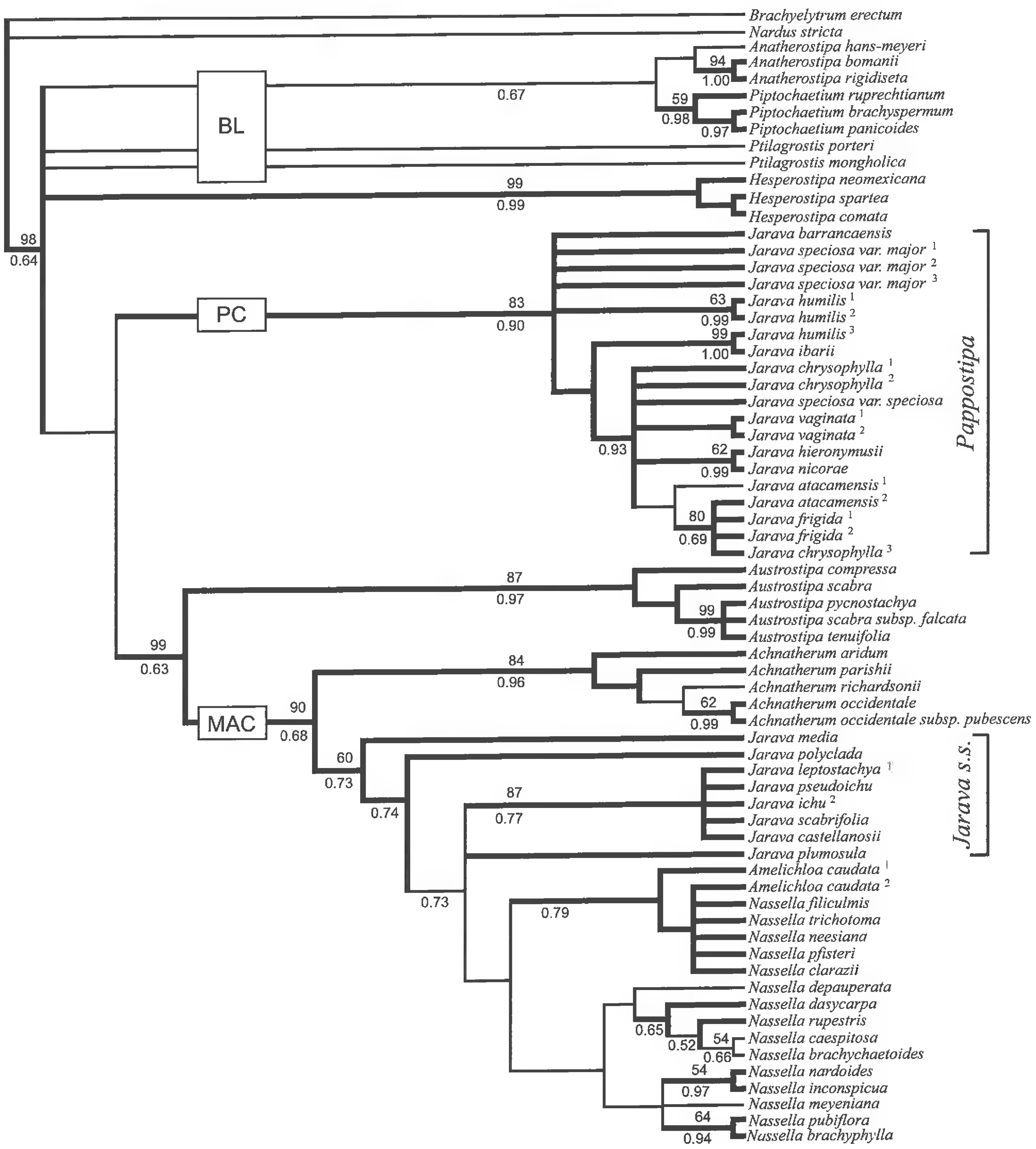

Fig. 1. Majority-rule consensus tree of 1001 most parsimonious trees based on maximum parsimony analysis of sequence data from chloroplast DNA *trn*K-*mat*K, *mat*K, *trn*H-*psb*A, and *trn*L-*trn*F regions. Branches in bold are present in the strict consensus tree, i.e. branch frequency (BF) equal to 100. Numbers above branches correspond to bootstrap (BS) values; numbers below branches correspond to Bayesian posterior probability (PP) values; BL=basal lineages; MAC=Major American Clade; PC=*Pappostipa* clade.

In the ITS and combined trees (Figs. 2 & 3) two major clades are resolved (with low support indices) within the *Pappostipa* clade: "P" that includes *Jarava barrancaensis, J. hieronymusii, J. nicorae, J. patagonica, J. speciosa* var. *major, J. speciosa* var. *speciosa*, and *J. vaginata* (BF=53, PP=<0.50–0.52); and "C" that includes *Jarava atacamensis, J. chrysophylla, J. frigida, J. humilis*, and *J. ibarii* (BF=97–100, PP=<0.50–0.90). Within all three trees (Figs. 1–3), *J. speciosa* var. *speciosa* and *J. speciosa* var. *major* never share a most-recent common

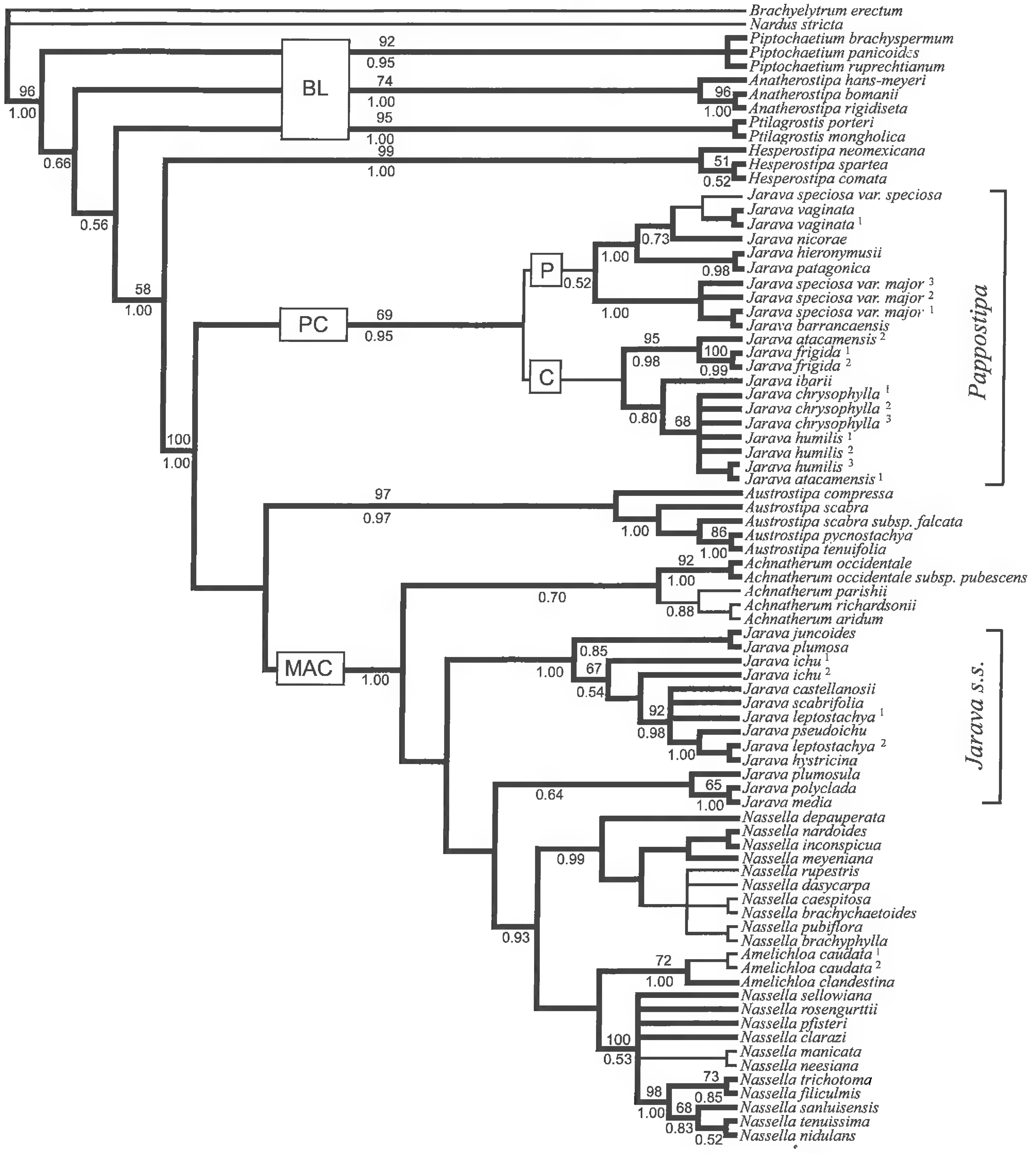

FIG. 2. Majority-rule consensus tree of 1001 equally most parsimonious trees based on maximum parsimony analysis of sequence data from nuclear rDNA ITS region. Branches in bold are present in the strict consensus tree, i.e., branch frequency (BF) equal to 100. Numbers above branches correspond to bootstrap (BS) values; numbers below branches correspond to Bayesian posterior probability (PP) values; BL=basal lineages; MAC=Major American Clade; PC=*Pappostipa* clade; C=*Pappostipa* sect. *Chrysovaginatae*; P=*Pappostipa* sect. *Pappostipa*.

ancestor. There is a distinct incongruence in the placement of *J. speciosa* var. *speciosa* in the plastid and nuclear trees (Figs. 1 & 2), but our plastid data currently provide little information on this discrepancy since there are only one or two apomophies found in the sequences of the *trn*L-F region.

In the three consensus trees (Figs. 1–3) MAC includes: a monophyletic *Achnatherum* (BF=100; PP=0.70–1.00; BS=84, <50, 76, respectively); a grade of four lineages (Fig. 1), two clades (Fig. 2), or a single clade (Fig. 3) for *Jarava*; and a single monophyletic clade of *Nassella* (including *Amelichloa*) (BF=61–100; PP

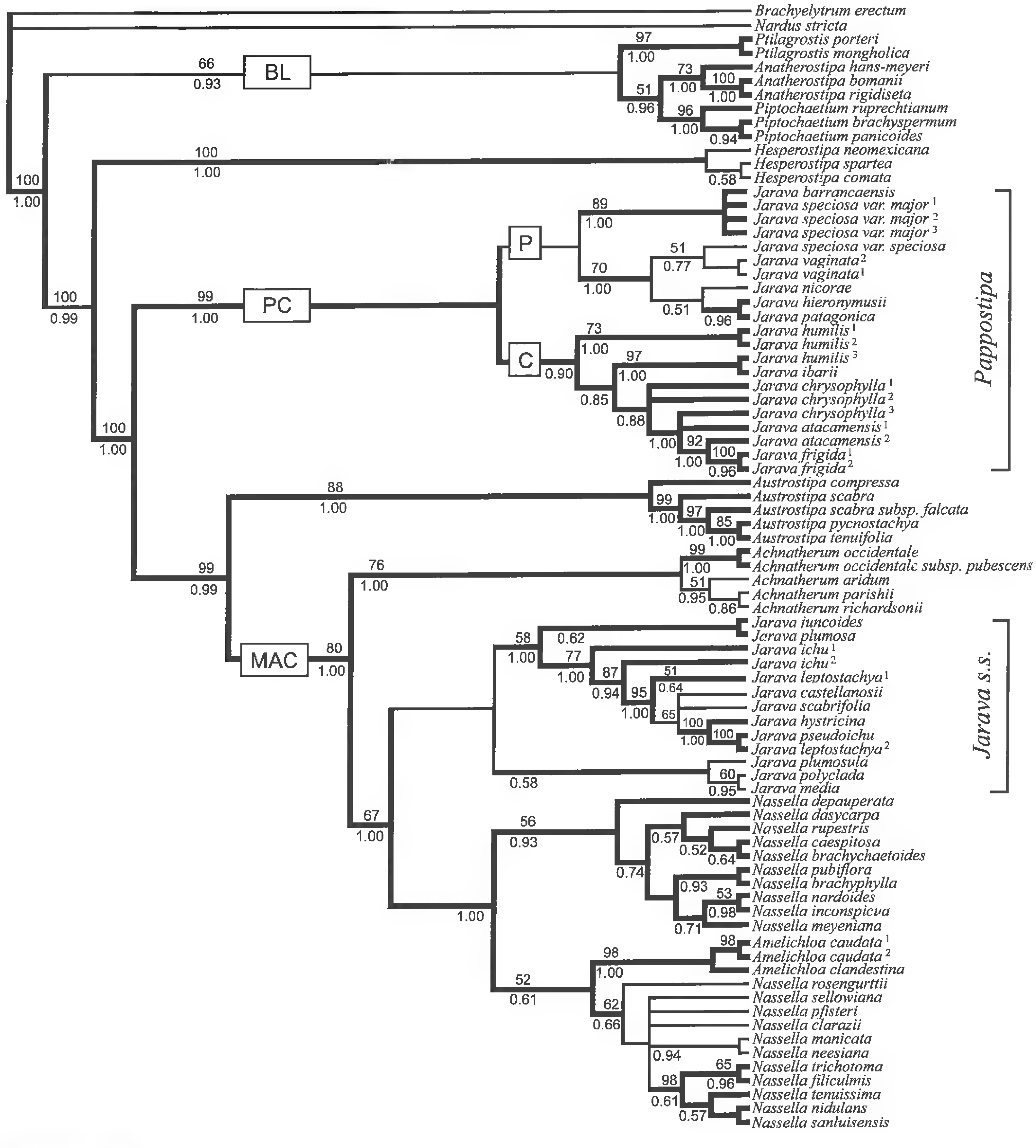

Fig. 3. Majority-rule consensus tree of 1001 equally most parsimonious trees based on maximum parsimony analysis of sequence data from chloroplast DNA *trnK-matK*, *matK*, *trnH-psbA*, and *trnL-trnF* regions and nuclear rDNA ITS region. Branches in bold are present in the strict consensus tree, i.e. branch frequency (BF) equal to 100. Numbers above branches correspond to bootstrap (BS) values; numbers below branches correspond to Bayesian posterior probability (PP) values; BL=basal lineages; MAC=Major American Clade; PC=*Pappostipa* clade; C=*Pappostipa* sect. *Chrysovaginatae*; P=*Pappostipa* sect. *Pappostipa*.

<0.50, 0.93, 1.00; Figs 2 & 3). *Jarava ichu*, the type species for the genus, resolved in a clade with *J. castellanosii*, *J. leptostachya*, *J. pseudoichu*, and *J. scabrifolia* in Fig. 1 (BF=100, PP=0.77, BS=87). Three *Jarava* species not in the plastid analysis, *J. hystercina*, *J. juncoides*, and *J. plumosa*, join the clade with the above set of species in Fig. 2 (BF=100, PP=1.00) and Fig. 3 (BF=100, PP=1.00, BS=58). In the combined analysis *Jarava media*, *J. plumulosa*, and *J. polyclada* are united as a sister clade to the above set (BF=100, PP= 0.58; Fig. 3). The latter three species formed a clade in the ITS analysis (BF=100, PP=0.64) that was sister group to *Nassella* includ-

ing *Amelichloa*, but were scattered elements of the grade of *Jarava* lineages leading to *Nassella* (including *Amelichloa*) represented in Fig. 1.

Our consensus trees indicate that *Nassella* is monophyletic (BF=61–100, PP=<0.50–1.00) only if *Amelichloa* is included. This conclusion is most strongly supported in the ITS and combined analyses (BF=100, PP 0.93–1.00). In our consensus trees there are two major clades within *Nassella*. One clade includes *N. brachychaetoides, N. brachyphylla, N. caespitosa, N. dasycarpa, N. depauperata, N. meyeniana, N. pubiflora, N. nardoises,* and *N. rupestris* (with *N. inconspicua* in Figs. 2 & 3; BF=100, PP= 0.93–0.99, BS=<50–56). The second clade includes *Amelichloa* species as sister group to the set of *N. clarazii, N. filiculmis, N. manicata, N. neesiana, N. nidulans, N. pfisteri, N. rosengurtii, N. sanluisensis, N. sellowiana, N. tenuissima,* and *N. trichotoma* (Figs. 2 & 3; BF=100, PP=0.53–0.66, BS=62–100), or *Amelichloa caudata*[1] as sister group to the set of *A. caudata*[2], *N. clarazii, N. filiculmis, N. neesiana, N. pfisteri, N. trichotoma,* and *A. clandestina* (Fig. 1; BF=100, PP=<0.50). *Amelichloa* is supported as monophyletic in the ITS and combined analyses (Figs. 2 & 3; BF=100, PP=100; BS=72–98).

Comparative morphology.—We evaluated a series of morphological and anatomical characters including: awn indumentum, form of the callus, lemma epidermis, and anatomy of the leaf blade in transverse section that differ among the hypothesized lineages of *Jarava* s.l. Nearly all samples of *Jarava* s.l. listed in Table 1 were surveyed and representative examples are given in Fig. 4. In addition, features of *Amelichloa* have also been evaluated.

Callus.—In the *Pappostipa* clade (Fig. 4A–C) the callus is acute to acuminate, sharp pointed; the angle between the callus base plane and floret axis is low; callus base is lanceolate; peripheral ring is marginiform, with proximal borders near one another, not fused nor thin, leaving an open foveola (literally, "small depression or scar"; the term used to name the section of conducting bundle at the base of the callus, but not only its open ventral part as it was for species resolved here in the *Pappostipa* clade by Roig 1964); distal, flat prow of the peripheral ring is not developed or is moderately developed. The foveola is fusiform or lanceolate, usually the same shape as the peripheral ring.

In the *Jarava ichu* group (Fig. 4D) the callus is short, truncate, blunt to acute; the angle between the callus base plane and floret axis is higher than in *Pappostipa* clade; callus base is obovate or ovate, rarely orbicular or lanceolate; peripheral ring is marginiform to flat, proximal borders not near each other, thinned and not fused, leaving the foveola open; distal, flat prow of the peripheral ring is not developed, inconspicuous or is slightly conspicuous. The foveola is obovate, ovate or orbicular, rarely lanceolate, and usually the same shape as the peripheral ring.

In *Jarava media, J. plumosula,* and *J. polyclada,* (Fig. 4E) the callus is acute, sharp pointed; the angle between the callus base plane and floret axis is high; callus base is ovate or acuminate, tapering to the relatively long but obtuse point; peripheral ring is flat or slightly marginiform, proximal borders joined, usually fused and not thinned, closing the foveola; distal, flat prow of the peripheral ring is well developed, characteristically fused at the base. The foveola is oval or orbicular and does not follow the shape of peripheral ring.

In *Amelichloa caudata* and *A. cladestina* (Fig. 4F) the callus is short, blunt; the angle between the callus base plane and floret axis is high; callus base is obovate or oblong; peripheral ring is conspicuously marginiform, proximal borders not near each other, thinned, leaving the foveola open; distal, flat prow of the peripheral ring is not developed or is inconspicuous. The foveola is oval or oblong ellipsoid and usually follows the shape of the peripheral ring.

Lemma epidermis.—In species of the *Pappostipa* clade (Fig. 4G) the epidermal fundamental cells regularly alternate with silica cells and are all approximately the same length or shorter than the silica cells; end walls are straight or slightly uneven, sidewalls slightly sinuate; silica bodies are oval to oblong rectangular, slightly unequal. In the *Jarava* s.s. group (Fig. 4H) the epidermal fundamental cells regularly alternate with silica cells and are considerably shorter than the silica cells (designated here as "maize" pattern); end walls are straight, sidewalls thin-walled, lacking silica, straight or slightly uneven; silica bodies are short rectangular, often equal. In *Amelichloa caudata* and *A. clandestina* (Fig. 4I) the epidermal fundamental cells are usually ir-

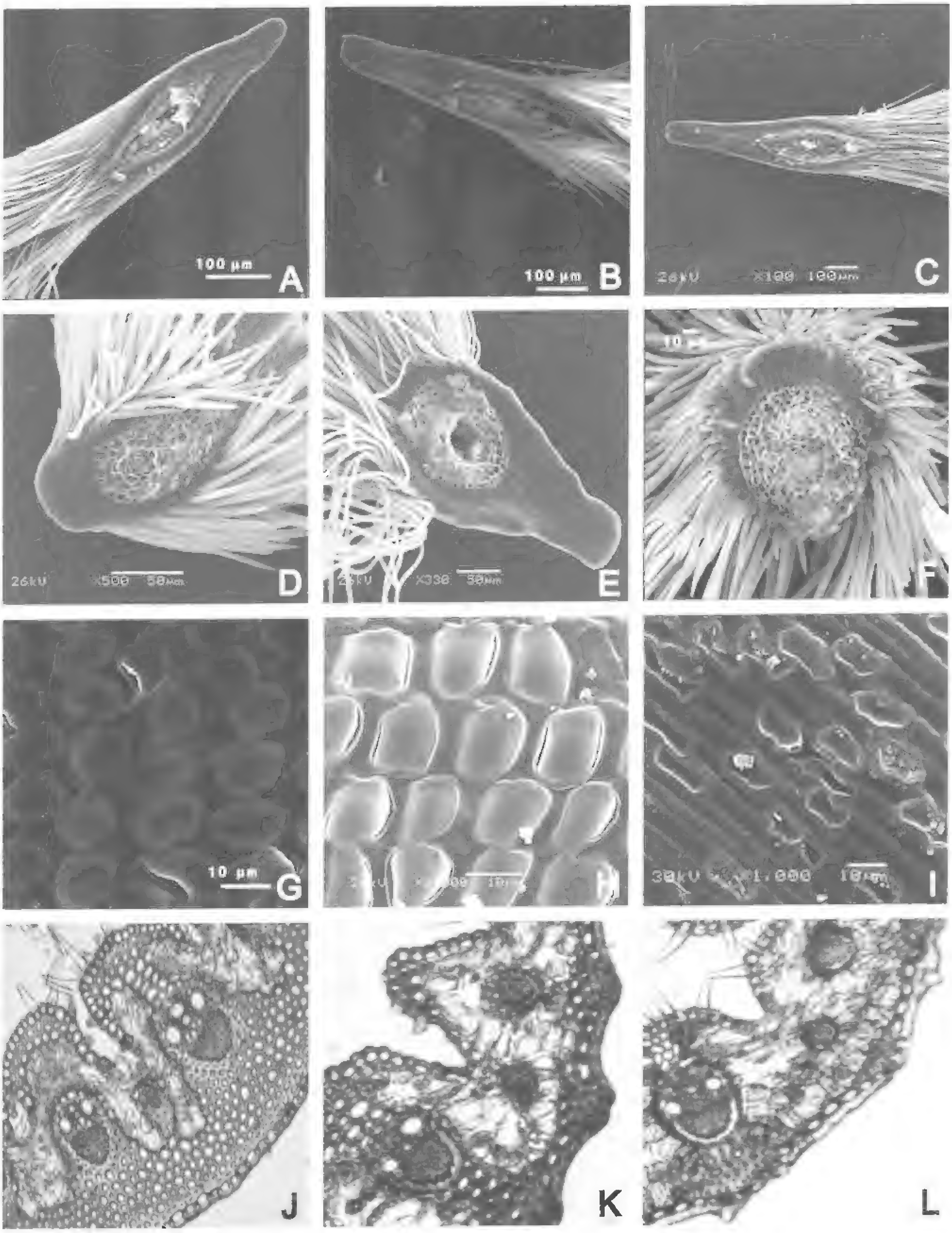

Fig. 4. Morphological and anatomical features of American Stipeae. **A.** Acute callus base of *Pappostipa chrysophylla* [*Peterson & Annable 11466* (US)]. **B.** Acute callus base of *Pappostipa speciosa* [*Peterson & Annable 11549* (US)]. **C.** Acute callus base of *Pappostipa nicorae* [*Peterson & Annable 11408* (US)]. **D.** Truncate callus base of *Jarava pseudoichu* [*Peterson, Soreng & Romaschenko 20471* (US)]. **E.** Acute callus base of *Jarava plumosula*.[*Peterson, Soreng & Romaschenko 20736* (US)]. **F.** Obovate callus base of *Amelichloa caudata* [*Peterson & Annable 11398* (US)]. **G.** Lemma epidermal fundamental cells are about the same size or shorter than the silica cells in *Pappostipa chrysophylla*. **H.** Lemma epidermal fundamental cells are larger than the silica cells in *Jarava pseudoichu*. **I.** Lemma epidermal fundamental cells are usually irregularly alternate with silica cells, and are shorter to approximately three times the length of the silica cells; endwalls are straight or slightly uneven, sidewalls sinuate in *Amelichloa caudata*. **J.** Basal leaf blade cross-section showing well developed adaxial ribs and furrows of *Pappostipa barrancaensis* [*Peterson & Annable 11371* (US)]. **K.** Basal leaf blade cross-section showing well developed adaxial ribs and furrows of *Pappostipa major* [*Soreng 7222* (US)]. **L.** Basal leaf blade cross-section showing inconspicuous ribs and furrows of *Pappostipa chrysophylla*.

regularly alternate with silica cells, and are shorter to approximately three times the length of the silica cells; end walls are straight or slightly uneven, sidewalls slightly sinuate; silica bodies are oblong, unequal.

Leaf blade transection.—Basal leaf blade cross-sections from *Jarava barrancaensis*, *J. speciosa* var. *major*, and *J. chrysophylla* are shown in Fig. 4J–L, and represent anatomical forms in the *Pappostipa* clade. We found two distinct types of leaf morphology and anatomy as detected by Arriaga (1983) that correspond with the two subclades **P** and **C** in our trees (Figs. 2&3). The P clade has type I leaf blade anatomy (incl. *Jarava barrancaensis*, *J. hieronymusii*, *J. nicorae*, *J. patagonica*, *J. speciosa* var. *major*, *J. speciosa* var. *speciosa*, and *J. vaginata*) with stiff, relatively thick usually pungent leaf apices, adaxial ribs well developed, separated by deep furrows; primary veins (vascular bundles) are numerous (5 or 6), often adaxially and abaxially connected by sclerenchyma girders (rarely by transitional parenchyma girders; Fig. 4J); tertiary veins are often abaxially connected by sclerenchyma girders; bulliform cells are present at the bottom of all furrows; abaxial sclerenchyma is continuous; adaxial sclerenchyma is discontinuous (Fig. 4K).

The C clade (Figs. 2&3) has type II leaf blade anatomy (incl. *Jarava atacamensis*, *J. frigida*, *J. humilis*, and *J. ibarii*) with slender, usually non-pungent leaf apices, adaxial ribs not well developed separated by shallow furrows; primary veins not numerous (1–3, rarely to 4), often only abaxially connected by sclerenchyma girders (rarely adaxially connected at the midrib); tertiary veins are often not connected by sclerenchyma; bulliform cells are present only close to the midrib; abaxial sclerenchyma is discontinuous; adaxial sclerenchyma is usually absent or residual (Matthei 1965; Arriaga 1983). *Jarava chrysophylla* (Fig. 4L) differs from the previous type by having clearly discontinuous abaxial sclerenchyma and tertiary veins that are adaxially connected by sclerenchyma girders in a compound midrib.

TAXONOMY

The phylogenetic information provided by our DNA analyses coupled with significant morphological differences among the *Jarava* s.l. clades detected, forces us to recognize the *Pappostipa* clade as an independently derived monophyletic genus if we are to maintain the monophyletic status of the other genera currently recognized in the AAAJN clade. Here we propose combinations in the new genus *Pappostipa* for all 14 species resolved in this clade in our DNA analyses, and *Stipa speciosa* f. *major* which is raised to the rank of species in *Pappostipa*. Eight additional species are transferred to *Pappostipa* that were formerly included in *Stipa* subg. *Pappostipa* by Parodi (1960) and or *Jarava* s.l. by Peñalillo (2002, 2003), based on their shared morphology with the DNA tested set of species. All currently accepted infraspecific taxa (Peñalillo 2003) in these 23 species are also transferred to *Pappostipa*. Leaf anatomy types described by Parodi (1960) and Arriaga (1983) correlated with the two *Pappostipa* subclades (P & C) detected in our DNA analysis. Further review of *Pappostipa* leaf blade and sheath morphology after our DNA analyses (based on Roig 1964, Nicora & Rúgolo de Agrasar 1978, and pers. obs.), continue to support this correlation. Therefore we conclude that *Pappostipa* can be divided into two morphologically distinct sections of 14 (*P.* sect. *Pappostipa*) and nine (*P.* sect. *Chrysovaginatae*) species.

Pappostipa (Speg.) Romaschenko, P.M. Peterson & Soreng, comb. et stat. nov. Basionym: *Stipa* subg. *Pappostipa* Speg., Anales Mus. Nac. Montevideo 4:III, 45. 1901. Synonym *Stipa* sect. *Papoforeas* E. Desv., Fl. Chil. 6:278. 1854. Type: *Stipa speciosa* Trin. & Rupr. (lectotype, designated here).

Plants perennial, caespitose, sometimes with stolons. Culms 10–70 cm long, erect or geniculate, with two or three nodes, often concealed by sheaths; basal branching intravaginal. Basal leaves (6–)10–40(–60) cm long, (0.5–)0.7–2.3(–2.5) wide, convolute, apices acuminate, sometimes pungent; adaxial surface pilose and sulcate, the furrows 8–13 or only 3–6; abaxial surface glabrous, scabrous, occasionally with macrohairs; sheaths glabrous or pubescent, open, whitish, pale or stramineous to brownish-red, reddish or purplish; ligules 0.5–1(–3) mm long, truncate, membranous, ciliate, or pilose. Flag leaves 4–15 cm long, sometimes deciduous; ligules 2–5 mm long, elongated. Panicles 30–240 mm long, with 5–50 spikelets, often compact, included or exserted in the upper leaf sheath; pedicels 0.5–12 mm long, often hairy. Glumes 15–45 mm long, subequal or slightly unequal, longer than floret, acuminate, hyaline, (1–)3–5-nerved, purplish, green-

ish, rarely plumbeous. Florets fusiform, terete. Calluses 1–4 mm long, often pilose, apex obtuse to truncate; foveolas proximally opened, often the shape of peripheral rings, fusiform or lanceolate; peripheral rings thickened near the margins, flat prow usually not developed. Lemmas 4–16(–17) mm long, chartaceous, entirely pubescent with short appressed hairs or dorsally glabrous along the upper ½ of the lemma, rarely hairs gradually elongate toward the base of the column or dorsally glabrous; prickles (hooks) usually present in the upper part; lobes up to 1 mm long; apices not fused into a crown. Awns 20–70(–193) mm long, persistent, once geniculate; columns 15–33 mm long, sometimes protruding above glumes, plumose, hairs 4–9 mm long; bristles 12–45(–170) mm long, equal to much longer than columns, scabrous, smooth or glabrous, sometimes pungent, pale to chestnut colored or black, straight, rarely sinuous or falcate. Paleas 4–13 mm long, usually subequal to lemmas, occasionally ½ as long as the lemmas or shorter, linear, linear-cuneate or elongate, hyaline, often dorsally hairy, exceptionally glabrous, two-nerved, rarely nerves extended as short awns, these not conspicuous. Lodicules 3. Stamens 3, anthers yellow or purplish.

Pappostipa sect. **Pappostipa,** sect. nov. Type: *Pappostipa speciosa* (Trin. & Rupr.) Romaschenko.

Pappostipa sect. *Pappostipa* differs from *P.* sect. *Chrysovaginatae* by having basal sheaths that are brownish-red, pink, or purplish and basal leaf blades that are stiff, relatively thick with pungent apices and usually with well developed adaxial ribs separated by deep furrows (referred to as type I leaf anatomy in Arriaga 1983).

"Short-bristle" group

The following species all share comparatively a short final segment of the awn (referred to as a bristle; Jacobs et al. 1995) that is 1.5–2 times shorter than the bristles in the "long-bristle" group, of *P.* sect. *Pappostipa*.

Pappostipa speciosa (Trin. & Rupr.) Romaschenko, comb. nov. Basionym: *Stipa speciosa* Trin. & Rupr., Sp. Gram. Stipac. 45. 1842. *Stipa humilis* var. *speciosa* (Trin. & Rupr.) Kuntze, Revis. Gen. Pl. 3(3):371. 1898. *Achnatherum speciosum* (Trin. & Rupr.) Barkworth, Phytologia 74:13. 1993. *Jarava speciosa* (Trin. & Rupr.) Peñailillo, Gayana, Bot. 59(1):32. 2002. Type: CHILE: *H. Cuming s.n.* (holotype: LE-TRIN-1443.01!; isotype: US-557434 fragm. ex LE!).

Pappostipa speciosa var. **manqueclensis** (F.A. Roig) Romaschenko, comb. nov. Basionym: *Stipa speciosa* var. *manqueclensis* F.A. Roig, Revista Fac. Ci. Agrar. Univ. Nac. Cuyo 12:89, t. 5. 1965. *Jarava speciosa var. manqueclensis* (F.A. Roig) Peñailillo, Contr. U.S. Natl. Herb. 48:407. 2003. Type: ARGENTINA: San Carlos, Pampa de Las Cortaderas, *F. Roig 5339* (holotype: MERL).

Pappostipa speciosa var. **atuelensis** (F.A. Roig) Romaschenko, comb. nov. Basionym: *Stipa speciosa* f. *atuelensis* F.A. Roig. Revista Fac. Ci. Agrar. Univ. Nac. Cuyo 12(1):91–94, lamina 6. 1–9. 1965. *Stipa speciosa* var. *atuelensis* (F.A. Roig) F.A. Roig, Deserta 2:113. 1971. *Jarava speciosa* var. *atuelensis* (F.A. Roig) Peñailillo, Contr. U.S. Natl. Herb. 48:407. 2003. Type: ARGENTINA. Mendoza: Depto. San Rafael, Sosneado, en márgenes del Río Atuel, *A. Ruiz Leal 23229* (holotype: MERL).

Pappostipa speciosa var. **parva** (F.A. Roig) Romaschenko, comb. nov. Basionym: *Stipa speciosa* var. *parva* F.A. Roig, Revista Fac. Ci. Agrar. Univ. Nac. Cuyo 11(1–2):33–35. 1964 [1966]. *Jarava speciosa* var. *parva* (F.A. Roig) Peñailillo, Contr. U.S. Natl. Herb. 48:407. 2003. Type: ARGENTINA: Las Heras, Paramillo de Uspallata, 2800m,18–19 Jan 1938, *A. Ruiz Leal 4880* (holotype: MERL).

Pappostipa speciosa var. **breviglumis** (Parodi) Romaschenko, comb. nov. Basionym: *Stipa speciosa* var. *breviglumis* Parodi, Revista Argent. Agron. 27(3–4):74, f. 1, B, b, i. 1960. *Jarava speciosa* var. *breviglumis* (Parodi) Peñailillo, Contr. U.S. Natl. Herb. 48:407. 2003. Type: ARGENTINA. San Juan: Depto. Iglesia, al norte de Rodeo, Mina Fierro Nuevo, 24 Feb 1950, *V.R. Perrone 54904 1/2* (holotype: BAA).

Pappostipa speciosa var. **ciliata** (F.A. Roig) Romaschenko, comb. nov. Basionym: *Stipa speciosa* var. *ciliata* F.A. Roig, Giorn. Bot. Ital. 121(1–2):43, f. 2. 1987.*Jarava speciosa* var. *ciliata* (F.A. Roig) Peñailillo, Contr. U.S. Natl. Herb. 48:407. 2003. Type: ARGENTINA. San Juan: Iglesia, entre Tocota y Cuesta de los Heladeros, 5 Mar 1962, 2180m, *A. Ruiz Leal 22093* (holotype: MERL; isotype: SI).

Pappostipa speciosa f. **horrida** (F.A. Roig) Romaschenko, comb. nov. Basionym: *Stipa speciosa* f. *horrida* F.A. Roig, Revista Fac. Ci. Agrar. Univ. Nac. Cuyo 11(1–2):36, t. 25a. 1964 [1966]. *Jarava speciosa* f. *horrida* (F.A. Roig) Peñailillo, Contr. U.S. Natl. Herb. 48:407. 2003. Type: ARGENTINA: Malalhue, Cerro Huemul, frecuente, matas aisladas, rígidas, pinchudas, 14 Jan 1958, *A. Ruiz Leal & F.A. Roig 18784* (holotype: MERL?).

Pappostipa speciosa f. **abscondita** (F.A. Roig) Romaschenko, comb. nov. Basionym: *Stipa speciosa* f. *abscondita* F.A. Roig, Revista Fac. Ci. Agrar. Univ. Nac. Cuyo 11(1–2):36–37. 1964 [1966]. *Jarava speciosa* f. *abscondita* (F.A. Roig) Peñailillo, Contr. U.S. Natl. Herb. 48:407. 2003. Type: ARGENTINA: Las Heras, Uspallata, Cumbre del Paramillo, 11 Feb 1964, *F.A.. Roig 4929* (holotype: MERL).

Pappostipa speciosa var. **media** (Torres) Romaschenko, comb. nov. Basionym: *Stipa speciosa* var. *media* Torres, Comis. Invest. Ci. [Buenos Aires] 12:44, t.1, C, c; t.4d. 1993. *Jarava speciosa* var. *media* (Torres) Peñailillo, Contr. U.S. Natl. Herb. 48:407. 2003. Type: ARGENTINA. Buenos Aires: Pdo. Villarino, Laguna Chasicó; 19 Apr 1976, *J. Frangi 79* (holotype: LP).

Pappostipa vaginata (Phil.) Romaschenko, comb. nov. Basionym: *Stipa vaginata* Phil., Linnaea 33(3–4):281. 1864. *Jarava vaginata* (Phil.) F. Rojas, Gayana, Bot. 54(2):173. 1997 [1998]. Type: CHILE. Aconcagua: S. Felipe, Nov 1862, *Landbeck s.n.* (holotype:?; isotypes: SGO-45662, US-81900 fragm. ex W!).

Pappostipa vaginata f. **rigida** (F.A. Roig) Romaschenko, comb. nov. Basionym: *Stipa vaginata* f. *rigida* F.A. Roig, Revista Fac. Ci. Agrar. Univ. Nac. Cuyo 11(1–2):54–55. 1964 [1966]. *Jarava vaginata* f. *rigida* (F.A. Roig) Peñailillo, Contr. U.S. Natl. Herb. 48:407. 2003. Type: ARGENTINA: Las Heras, Paramillo de Uspallata, Cumbre del Paramillo, 2850m, 11 Feb 1964, *F.A. Roig 4927* (holotype: ?; isotype: LP).

Pappostipa vaginata f. **inmersa** (F.A. Roig) Romaschenko, comb. nov. Basionym: *Stipa vaginata* f. *inmersa* F.A. Roig, Revista Fac. Ci. Agrar. Univ. Nac. Cuyo 11(1–2):53–54, t. 10 & 25e. 1964 [1966]. *Jarava vaginata* f. *inmersa* (F.A. Roig) Peñailillo, Contr. U.S. Natl. Herb. 48:407. 2003. Type: ARGENTINA: Las Heras, Cumbre del Paramillo de Uspallata, 2800m, 22 Jan 1960, *F.A. Roig 4319* [*F.A. Roig 4308* cited also in parentheses with 4319] (holotype: MERL?; isotype: LP).

Pappostipa vaginata f. **laevis** (F.A. Roig) Romaschenko, comb. nov. Basionym: *Stipa vaginata* f. *laevis* F.A. Roig, Revista Fac. Ci. Agrar. Univ. Nac. Cuyo 11(1–2): 52, t. 10 & 25g. 1964 [1966]. *Jarava vaginata* f. *laevis* (F.A. Roig) Peñailillo, Contr. U.S. Natl. Herb. 48:407. 2003. Type: ARGENTINA: Las Heras, Paramillo de Uspallata, 2800m, 22 Jan 1960, *F.A. Roig & A. Ruiz Leal 4318* (holotype: MERL?).

Pappostipa vaginata f. **contracta** (F.A. Roig) Romaschenko, comb. nov. Basionym: *Stipa vaginata* f. *contracta* F.A. Roig, Revista Fac. Ci. Agrar. Univ. Nac. Cuyo 11(1–2):53, t. 10 & 25f. 1964 [1966]. *Jarava vaginata* f. *contracta* (F.A. Roig) Peñailillo, Contr. U.S. Natl. Herb. 48:407. 2003. Type: ARGENTINA: Las Heras, Los Hornillos, 10 Jan 1959, *A. Ruiz Leal 20144* (holotype: MERL herb. F.A. Roig 3405; isotype: LP).

Pappostipa vaginata var. **argyroidea** (F.A. Roig) Romaschenko, comb. nov. Basionym: *Stipa vaginata* var. *argyroidea* F.A. Roig, Deserta 2:107, t. 1. 1971.*Jarava vaginata* var. *argyroidea* (F.A. Roig) Peñailillo, Contr. U.S. Natl. Herb. 48:407. 2003. Type: ARGENTINA. Mendoza: Depto. Malalhue, entre Cañada Colorada y Fortín Malalhue, 9 Nov 1960, *F.A. Roig 4514* (holotype: MERL?; isotype: LP ex Herb. Roig 4514).

Pappostipa vaginata var. **dilatata** (F.A. Roig) Romaschenko, comb. nov. Basionym: *Stipa vaginata* var. *dilatata* F.A. Roig, Revista Fac. Ci. Agrar. Univ. Nac. Cuyo 11(1–2):54. 1964 [1966]. *Jarava vaginata* var. *dilatata* (F.A. Roig) Peñailillo, Contr. U.S. Natl. Herb. 48:407. 2003. Type: ARGENTINA: Las Heras, Camino a Uspallata por Potrerillos, ala vera del mismo, en suelos removidos, arenosos, 22 Dec 1961, *A. Ruiz Leal, Roig & Wainstein 4523* (holotype: ?; isotype: LP).

Pappostipa nicorae (F.A. Roig) Romaschenko, comb. nov. Basionym: *Stipa nicorae* F.A. Roig, Giorn. Bot. Ital. 121(1–2):41, f. 1. 1987. *Jarava* nicorae (F.A. Roig) Peñailillo, Gayana, Bot. 59(1):32. 2002. Type: ARGENTINA. San Juan: Depto. Iglesia, Reserva de San Guillermo, Cajoncito de la Brea al N del Infiernillo, 3680m, 20 Feb 1981, *E. Nicora, Guaglianone & Ragonese 8201* (holotype: SI; isotype: LP).

Pappostipa hieronymusii (Pilg.) Romaschenko, comb. nov. Basionym: *Stipa hieronymusii* Pilg., Bot. Jahrb. Syst. 56 (Beibl. 123):24. 1920. *Jarava hieronymusii* (Pilg.) Peñailillo, Gayana, Bot. 59(1):31. 2002. Type: ARGENTINA. La Rioja: Depto. Gral. Sarmiento, Cuesta del Peñón al sur de la Laguna Brava, Cordillera de La Rioja, 26 Feb 1879, *G. Hieronymus & G. Niederlein 314* (holotype: B; isotypes: BAA-3071 fragm. ex B, CORD, US-866109 fragm!).

Pappostipa patagonica (Speg.) Romaschenko, comb. nov. Basionym: *Stipa patagonica* Speg., Revista Fac. Agron. Veterin. (Buenos Aires) 3:581. 1897. *Jarava patagonica* (Speg.) Peñailillo, Gayana, Bot. 59(1):32. 2002. Type: ARGENTINA. Santa Cruz: Río Santa Cruz, Feb 1882, *C. Spegazzini s.n.* (lectotype: LP ex LPS-2433 designated by L.R. Parodi, Revista Argent. Agron. 27(3–4):72. 1960; isolectotypes: BAA, LPS).

Pappostipa maeviae (F.A. Roig) Romaschenko, comb. nov. Basionym: *Stipa maeviae* F.A. Roig, Bol. Soc. Argent. Bot. 14(4):314, f. 2. 1972. *Jarava maeviae* (F.A. Roig) Peñailillo, Gayana, Bot. 59(1):31. 2002. Type: ARGENTINA. Neuquén: Depto. Chos Malal, filo SE del volcán Domuyo, en pedregales, s. d., *O. Boelck 11290* (holotype: BAA; isotype: BAB).

Pappostipa parodiana (F.A. Roig) Romaschenko, comb. nov. Basionym: *Stipa parodiana* F.A. Roig, Revista Fac. Ci. Agrar. Univ. Nac. Cuyo 11(1–2):44–46, t. 8, 26b. 1964 [1966]. *Jarava parodiana* (F.A. Roig) Peñailillo, Gayana, Bot. 59(1):31. 2002. Type: ARGENTINA: Malalhue, Ranquil de Lirkai, 1100m, frecuente en las laderas empinadas de los cerros, 14 Dec 1960, *A. Ruiz Leal 21453* (holotype: MERL).

Pappostipa braun-blanquetii (F.A. Roig) Romaschenko, comb. nov. Basionym: *Stipa braun-blanquetii* F.A. Roig, Phytocoenologia 2(1–2):19, f. 1. 1975. *Jarava braun-blanquetii* (F.A. Roig) Peñailillo, Contr. U.S. Natl. Herb. 48:407. 2003. Type: ARGENTINA. Mendoza: San Rafael, Valle de Las Leñas, 13 Jan 1970, A. Ruiz Leal 27150 (holotype: MERL; isotype: LP).

Pappostipa semperiana (F.A. Roig) Romaschenko, comb. nov. Basionym: *Stipa semperiana* F.A. Roig, Revista Fac. Ci. Agrar. Univ. Nac. Cuyo 11(1–2):37t. 6, 25d. 1964 [1966]. *Jarava semperiana* (F.A. Roig) Peñailillo, Gayana, Bot. 59(1):31. 2002. Type: ARGENTINA: Las Heras, entre Uspallata y Puesto San Alberto (La Arboleda), 27 Dec 1947, *A. Ruiz Leal 11138* (holotype: MERL).

Pappostipa ruiz-lealii (F.A. Roig) Romaschenko, comb. nov. Basionym: *Stipa ruiz-lealii* F.A. Roig, Revista Fac. Ci. Agrar. Univ. Nac. Cuyo 11(1–2):42, t. 5, 25c. 1964 [1966]. *Jarava ruiz-lealii* (F.A. Roig) Peñailillo, Gayana, Bot. 59(1):31. 2002. Type: ARGENTINA: Las Heras, Paramillo de Uspallata, 2800m, 23 Jan 1960, *A. Ruiz Leal & F.A. Roig 20774* (holotype: MERL-20774).

"Long-bristle" group

The following four species all share the unique characteristic of having the final segment of the awn (referred to as a bristle; Jacobs et al. 1995) as being 1.5–2 times longer than the bristles in the "short-bristle" group of species of *P.* sect. *Pappostipa*.

Pappostipa malalhuensis (F.A. Roig) Romaschenko, comb. nov. Basionym: *Stipa malalhuensis* F.A. Roig, Revista Fac. Ci.

Agrar. Univ. Nac. Cuyo 11(1–2):60–62, t, 13, 25d. 1964 [1966]. *Jarava malalhuensis* (F.A. Roig) Peñailillo, Gayana, Bot. 59(1):31. 2002. Type: ARGENTINA: Malalhue, Potí Malal, n.v. "coirón blanco," 13 Jan 1960, *A. Ruiz Leal 20938* (holotype: MERL-20938).

Pappostipa major (Speg.) Romaschenko, comb. et stat. nov. Basionym: *Stipa speciosa* f. *major* Speg., Anales Mus. Nac. Montevideo 4(2):58, f. 10a–b. 1901. *Stipa speciosa* var. *major* (Speg.) Parodi, Revista Argent. Agron. 27(3–4): 75, f. 1, C, c. 1960. *Jarava speciosa* var. *major* (Speg.) Peñailillo, Contr. U.S. Natl. Herb. 48:407. 2003. Type: ARGENTINA: vulgato prope Lago Nahuel-huapi, Jan 1900, *E. Fernádez s.n.* (syntype: ?). Neuquen: in Valle Trolope, Feb 1900, *Otto Asp s.n.* (syntype: ?).

Pappostipa major can be separated from *P. speciosa* by having longer glumes, narrower and convolute leaf blades, longer bristles usually 1.5 to 2 times as long, black (yellow in *P. speciosa*) bristles, larger anthecia, and a chromosome base number of 2*n*=60 (2*n*=66 in *P. speciosa*) [Parodi 1960; Stebbins & Löve 1941; Covas & Bocklet 1945]. Futhermore, these varieties were resolved independently of one another in both the plastid and ITS DNA analyses (**Figs. 1, 2 & 3**).

Pappostipa vatroensis (F.A. Roig) Romaschenko, comb. nov. Basionym: *Stipa vatroensis* F.A. Roig, Revista Fac. Ci. Agrar. Univ. Nac. Cuyo 11(1–2):40–42, t. 7, 26a. 1964 [1966]. *Jarava vatroensis* (F.A. Roig) Peñailillo, Gayana, Bot. 59(1): 31.2002. Type: ARGENTINA: Malalhue, el Vatro, 1100m, en la margen izquierda del río Barrancas, en laderas, 16 Dec 1960, *A. Ruiz Leal 21501* = *F.A. Roig 3765* (holotype: MERL).

Pappostipa barrancaensis (F.A. Roig) Romaschenko, comb. nov. Basionym: *Stipa vatroensis* F.A. Roig, Revista Fac. Ci. Agrar. Univ. Nac. Cuyo 11(1–2):40–42, t. 7, 26a. 1964 [1966]. *Jarava barrancaensis* (F.A. Roig) Peñailillo, Gayana, Bot. 59(1):31. 2002. Type: ARGENTINA: Malalhue, el Vatro, 1100m, en la margen izquierda del río Barrancas, en laderas, 16 Dec 1960, *A. Ruiz Leal 21501* = *F.A. Roig 3765* (holotype: MERL).

Pappostipa sect. **Chrysovaginatae** Romaschenko, sect. nov. Type: *Pappostipa chrysophylla* (E. Desv.) Romaschenko.

A *Pappostipa* sect. *Pappostipa* imis vaginis pallidis vel pauce aurantis (non rubro-fuscis) et imis foliis tenuis et fasciculatis, non coriaceis, setaceis (valde acutis, sed non pungentibus), verticalibus, convolutis (teretibus in trans-sectione), et cum non profundibus adaxialibus sulcis.

Pappostipa sect. *Chrysovaginatae* differs from *P.* sect. *Pappostipa* by having pale or stramineous to golden, basal sheaths and basal leaves that are thin and not coriaceous, setaceous (sharply pointed but not pungent), straight, convolute (terete in cross section), and with shallow adaxial furrows. All species have type II leaf anatomy as described by Arriaga (1983).

Pappostipa sorianoi (Parodi) Romaschenko, comb. nov. Basionym: *Stipa sorianoi* Parodi, Revista Argent. Agron. 27(3–4):94, f. 5, B, b–e. 1960. *Jarava sorianoi* (Parodi) Peñailillo, Gayana, Bot. 59(1):31. 2002. Type: ARGENTINA. Santa Cruz: 20 km al norte de Perito Moreno, 13 Dec 1954, *A. Soriano 4775* (holotype: BAA!).

Pappostipa atacamensis (Parodi) Romaschenko, comb. nov. Basionym: *Stipa atacamensis* Parodi, Revista Argent. Agron. 27(3–4):85, f. 3. 1960 [1961]. *Jarava atacamensis* (Parodi) Peñailillo, Gayana, Bot. 59(1):31. 2002. Type: CHILE. Atacama: Depto. Copiapó, Quebrada de Plaza, 3600m, 4 Feb 1949, *A. Krapovickas & J. Hunziker 5789* (holotype: BAA-2964; isotypes: CONC-29647, SGO-73250).

Pappostipa nana (Speg.) Romaschenko, comb. nov. Basionym: *Stipa nana* Speg., Revista Argent. Bot. 1:23. 1925. *Jarava nana* (Speg.) Peñailillo, Gayana, Bot. 59(1):31. 2002. Type: ARGENTINA. Santa Cruz: 1/2 legua al S de la laguna de Sehuenaiken, 3 Feb 1903, *C. Spegazzini s.n.* (holotype: LP ex LPS-2501).

Pappostipa ibarii (Phil.) Romaschenko, comb. nov. Basionym: *Stipa ibarii* Phil., Anales Univ. Chile 93:716. 1896. *Jarava ibarii* (Phil.) Peñailillo, Gayana, Bot. 59(1):31. 2002. Type: CHILE: Patagonia ad lacum Pinto, Dec 1877, *H. Ibar s.n.* (holotype: SGO-45658; isotypes: B, BAA-3092 fragm. ex B, SGO-62799, US-1762378 fragm. ex SGO!, US-141625 fragm!, US-photo ex SGO-45658!).

Pappostipa ibarii f. **pallescens** (Parodi) Romaschenko, comb. nov. Basionym: *Stipa ibarii* f. *pallescens* Parodi, Revista Fac. Ci. Agrar. Univ. Nac. Cuyo 11(1–2):55–57, t. 11. 1964. *Jarava ibarii* f. *pallescens* (Parodi) Peñailillo, Contr. U.S. Natl. Herb. 48:407. 2003. Type: ARGENTINA: Las Heras, Paramillo de Uspallata, entre 2600–2800m, 18–19 Feb 1938, *A. Ruiz Leal 4830* (holotype: BAA).

Pappostipa ibarii var. **anomala** (Parodi) Romaschenko, comb. nov. Basionym: *Stipa ibarii* var. *anomala* Parodi, Revista Argent. Agron. 27(3–4):89. 1960. *Jarava ibarii* var. *anomala* (Parodi) Peñailillo, Contr. U.S. Natl. Herb. 48:407. 2003. Type: ARGENTINA. Santa Cruz: Depto. Río Chico, Gdor. Gregores, *A. Soriano 5080* (holotype: BAA).

Pappostipa ameghinoi (Speg.) Romaschenko, comb. nov. Basionym: *Stipa ameghinoi* Speg., Anales Mus. Nac. Montevideo 4(2):163–165, f. 50. 1901. *Jarava ameghinoi* (Speg.) Peñailillo, Gayana, Bot. 59(1):31. 2002. Type: ARGENTINA. Santa Cruz: Golfo San Jorge, Aest. 1899, *C. Ameghino s.n.* (holotype: LP-12593 ex LPS).

Pappostipa ameghinoi var. **digona** (Parodi) Romaschenko, comb. nov. Basionym: *Stipa ameghinoi* var. *digona* Parodi, Revista Argent. Agron. 27(3–4):80, f. 2. 1960. *Jarava ameghinoi* var. *digona* (Parodi) Peñailillo, Contr. U.S. Natl. Herb. 48:407. 2003. Type: ARGENTINA. Santa Cruz: Chicorikaike, 50° S 69° 25' W, Jan 1930, *A. Renard 13* (holotype: BAA).

Pappostipa ameghinoi var. **precordillerana** (F.A. Roig) Romaschenko, comb. nov. Basionym: *Stipa ameghinoi* var. *precordillerana* F.A. Roig, Revista Fac. Ci. Agrar. Univ. Nac. Cuyo 12(1):79, 80–81, t. 1. 1965. *Jarava ameghinoi* var. *precordillerana*

(F.A. Roig) Peñailillo, Contr. U.S. Natl. Herb. 48:407. 2003. Type: ARGENTINA. Mendoza: Las Heras, Alto de los Manantiales, 20 Feb 1965, *F.A. Roig 5284* (holotype: MERL; isotype: LP).

Pappostipa chubutensis (Speg.) Romaschenko, comb. nov. Basionym: *Stipa chubutensis* Speg., Anales Mus. Nac. Montevideo 4(2):49–51, f. 7. 1901. *Jarava chubutensis* (Speg.) Peñailillo, Gayana, Bot. 59(1):31. 2002. Type: ARGENTINA. Chubut: Teka Choque, Feb 1900, *O. Mauri s.n.* (holotype: BAA ex LPS-2477; isotypes: US-1721311!, US-141588!).

Pappostipa chubutensis var. **hirsutissima** (F.A. Roig) Romaschenko, comb. nov. Basionym: *Stipa chubutensis* var. *hirsutissima* F.A. Roig, Bol. Soc. Argent. Bot. 14(4):316, f. 3. 1972. *Jarava chubutensis* var. *hirsutissima* (F.A. Roig) Peñailillo, Contr. U.S. Natl. Herb. 48:407. 2003. Type: ARGENTINA. Santa Cruz: Depto. Puerto Deseado, 30 km al S de Puerto Deseado por ruta 282, 20 Nov 1963, *Correa et al. 2638* (holotype: BAA; isotypes: BAA-BAB, LP).

Pappostipa frigida (Phil.) Romaschenko, comb. nov. Basionym: *Stipa frigida* Phil., Fl. Atacam. 54. 1860. *Jarava frigida* (Phil.) F. Rojas, Gayana, *Bot.* 54(2):173. 1997 [1998]. Type: CHILE: cerro Altos de Puquios, ca. 3810m, Feb. 1864, *Philippi s.n.* (holotype: SGO-63153).

Pappostipa frigida var. **parvispicula** (Parodi) Romaschenko, comb. nov. Basionym: *Stipa frigida* var. *parvispicula* Parodi, Revista Argent. Agron. 27(3–4):91, f. 4, E, e. 1960. *Jarava frigida* var. *parvispicula* (Parodi) Peñailillo, Contr. U.S. Natl. Herb. 48:407. 2003. Type: ARGENTINA. La Rioja: Depto Sarmiento, Paso de Pircas Negras, 4100m, en el límite Argentino–Chileno, 6 Feb 1949, *A. Krapovickas & J. Hunziker 5798* (holotype: BAA; isotypes: BAB, CORD).

Pappostipa humilis (Cav.) Romaschenko, comb. nov. Basionym: *Stipa humilis* Cav., Icon. 5:41, t. 466, f. 1. 1799. *Jarava humilis* (Cav.) Peñailillo, Gayana, Bot. 59(1):31. 2002. Type: CHILE: Puerto Deseado, "Habitat in Americae meridionalis portu vulgo Deseado in solo arido, floretque Decembri, Luis Née s.n.," *Nee s.n.* (holotype: MA; isotypes: SGO photo, US-866105 fragm!).

Pappostipa humilis var. **decrescens** (Kuntze) Romaschenko, comb. nov. Basionym: *Stipa humilis* var. *decrescens* Kuntze, Revis. Gen. Pl. 3(3):371. 1898. *Jarava humilis* var. *decrescens* (Kuntze) Peñailillo, Contr. U.S. Natl. Herb. 48:407. 2003. Type: ARGENTINA: Patagonia, Paso Cruz, 2000m, 1 Apr 1882, *Moreno & Tonini 285* (syntype: NY!; isosyntype: US-A866104 ex NY!).

Pappostipa humilis var. **ruiziana** (Parodi) Romaschenko, comb. nov. Basionym: *Stipa humilis* var. *ruiziana* Parodi, Revista Argent. Agron. 27(3–4):104. 1960. *Jarava humilis* var. *ruiziana* (Parodi) Peñailillo, Contr. U.S. Natl. Herb. 48:407. 2003. Type: ARGENTINA. Mendoza: Depto. Las Heras, cerca de Hornillos, abundante, 21 Jan 1944, *A. Ruiz Leal 8593* (holoytpe: BAA).

Pappostipa chrysophylla (E. Desv.) Romaschenko, comb. nov. Basionym: *Stipa chrysophylla* E. Desv., Fl. Chil. 6:278, t. 76, f. 2. 1854. *Stipa humilis* f. *chrysophylla* (E. Desv.) Kuntze, Revis. Gen. Pl. 3(3):371. 1898. *Stipa speciosa* subsp. *chrysophylla* (E. Desv.) Dusén, Rep. Princeton Univ. Exp. Patagonia, Bot., Suppl. 8(3):30–31. 1914 [1915]. *Jarava chrysophylla* (E. Desv.) Peñailillo, Gayana, Bot. 59(1):31. 2002. Type: CHILE: Coquimbo, en el valle de Toro a 3497m, sobre un terreno de fonolito, y en el de los Patos, *C. Gay 376* (syntype: P; isosyntype: US-866134!). CHILE: Habita en los helechos de los cordilleras altas de Guanta a 2003m, y también en Copiapó, *Gay s.n.* (syntype: ?).

Pappostipa chrysophylla f. **minuta** (F.A. Roig) Romaschenko, comb. nov. Basionym: *Stipa chrysophylla* f. *minuta* F.A. Roig, Revista Fac. Ci. Agrar. Univ. Nac. Cuyo 11(1–2):66, t. 25b. 1964 [1966]. *Jarava chrysophylla* f. *minuta* (F.A. Roig) Peñailillo, Contr. U.S. Natl. Herb. 48:407. 2003. Type: ARGENTINA: Malalhue, Los Molles, 1850–1950m, césped pequeño, hojas erectas, 11–22 Feb 1960, *A. Ruiz Leal 20847* (holotype: MERL?).

Pappostipa chrysophylla var. **cordillerarum** (Parodi) Romaschenko, comb. nov. Basionym: *Stipa chrysophylla* var. *cordillerarum* Parodi, Revista Argent. Agron. 27(3–4):99. 1960. *Jarava chrysophylla* var. *cordillerarum* (Parodi) Peñailillo, Gayana, Bot. 59(1):31. 2002. Type: ARGENTINA. La Rioja: Depto. Sarmiento, quebrada de las Cuevas, dominante en las laderas a 3900m, *A. Krapovickas & J. Hunziker 5855* (holotype: BAA; isotype: CORD).

Pappostipa chrysophylla var. **crispula** (Kuntze) Romaschenko, comb. nov. Basionym: *Stipa humilis* f. *crispula* Kuntze, Revis. Gen. Pl. 3(3):371. 1898. *Stipa chrysophylla* var. *crispula* (Kuntze) Parodi, Revista Argent. Agron. 27(3–4):98. 1960. *Jarava chrysophylla* var. *crispula* (Kuntze) Peñailillo, Contr. U.S. Natl. Herb. 48:407. 2003. Type: ARGENTINA: Paso Cruz, Cordillera, 34°N, 1500m, 1 Jan 1892, *C.E.O. Kuntze 72* (holotype: NY!).

Pappostipa chrysophylla f. **modica** (F.A. Roig) Romaschenko, comb. nov. Basionym: *Stipa chrysophylla* f. *modica* F.A. Roig, Revista Fac. Ci. Agrar. Univ. Nac. Cuyo 11(1–2):66–67. 1964 [1966]. *Jarava chrysophylla* f. *modica* (F.A. Roig) Peñailillo, Contr. U.S. Natl. Herb. 48:407. 2003. Type: ARGENTINA: Las Heras, Paramillo de Uspallata, 2800m, 9–11 Feb 1964, *A. Ruiz Leal 23249* (holotype: MERL?).

DISCUSSION

Basal lineages.—In order to focus on *Jarava* s.l. and the major American lineages of the Stipeae in the present paper we have excluded all except representatives of two extra-American lineages (i.e., one Asian *Ptilagrostis* and five species of the Australian genus *Austrostipa)* of Stipeae from our DNA analyses. Several small American genera were excluded from the present paper as they were not considered to be pertinent to the subjects of the present paper (see Methods), but they will be treated in subsequent publications. The phylogenetic patterns we detected with the present data are consistent with those detected with our larger worldwide dataset for Stipeae (preliminary ITS plastid analysis presented by Romaschenko et al. 2007; and

unpublished chloroplast DNA data). Because our taxon sampling here is purposefully curtailed, discussions of the basal radiations in the tribe are necessarily restrained in this paper. Since there is a larger phylogenetic story in the full dataset, not too much should be read into the placement of *Austrostipa* by itself as sister to the Major American Clade (MAC) in which, *Achnatherum*, *Jarava* s.s., *Nassella*, and *Amelichloa* are included. Nevertheless, some things can be said about the basal lineages as resolved here.

The early diverging or sister group position of the basal lineages (here *Piptochaetium*, *Ptilagrostis,* and *Anatherostipa*) in relation to *Achnatherum, Amelichloa, Austrostipa, Jarava* s.l., and *Nassella* [AAAJN] has never been indicated in previous reconstructions of the phylogeny of the Stipeae. An early diverging position of *Piptochaetium* (as a part of a complex of North American *Piptatherum/Oryzopsis* plus *Piptochaetium*) within Stipeae was reported by Jacobs et al. (2000) based on ITS sequence analysis. However, the authors assigned more weight to morphological similarities of this group with *Nassella* and consequently the early diverging position of *Piptochaetium* was thought to be an artifact. The early diverging position of *Piptochaetium* also was not recognized when a larger data set was used (Jacobs et al. 2007). Various morphological characters, such as: short, obovate floret, eccentric straight hairless awns, development of a crown, bulbous-based hairs on the apex of the lemma, silicified walls of fundamental cells of the lemma epidermis, and type of epiblast has suggested a close relationship between *Piptochaetium* and *Nassella* (Thomasson 1978; Barkworth & Everett 1987; Barkworth 1990, 1993; Jacobs et al. 2000; Barkworth & Torres 2001; Cialdella & Giussani 2002). In contrast to these conclusions, our data support a monophyletic origin of *Piptochaetium* near the base of the American Stipeae, thereby rendering *Nassella* and *Piptochaetium* as distant relatives. An independent origin of the above suite of characters in *Piptochaetium,* well removed from *Nassella*, is in agreement with the latest revision of *Piptochaetium* based on phylogenetic analysis of plastid *trn*L-F and *rpl*16 sequences and morphological characters (Cialdella et al. 2007).

All three genera of our "basal lineages" set (i.e.; *Piptochaetium*, *Ptilagrostis,* and *Anatherostipa*) have a "saw" like pattern on the lemma fundamental cells, where the side walls are usually much longer than end walls, strictly sinuate, lobate or dentate, and fundamental cells do not regularly alternate with silica cells (Barkworth 1983; Barkworth & Everett 1987). This lemma epidermal pattern is evidently the plesiomorphic condition in Stipeae and can be assumed to be an unspecialized characteristic within the Pooideae since no other pattern has been detected so far in mid to early fossil stipoid grasses (Thomasson 1978, 1980, 1981, 1982, 1985). There are unambiguously identifiable fossils from the Oligocene of the Stipeae called *Berriochloa* M.K. Elias with a "saw" like pattern in the lemma epidermis. Some early Pliocene fossils referred to *Nassella* (Thomasson 1978) have short fundamental cells but still have sinuate sidewalls and end walls like the basal lineages identified here, such as *Piptochaetium* but unlike extant species of *Nassella*.

Our molecular analyses indicate that *Ptilagrostis* and *Achnatherum* are also phylogenetically distant. This conclusion is further supported with micromorphological data, as the two genera have different lemma epidermal patterns (Barkworth 1983; Barkworth & Everett 1987). Based on the topology of our trees (Figs. 1–3), the polarization of the epidermal characters from *Achnatherum* (as a conditionally ancient state) to *Ptilagrostis* (as a conditionally derived state), as proposed Tzvelev (1977) and Barkworth and Everett (1987), is not parsimonious. We deduce that *Ptilagrostis* has the ancestral conditions for epidermal characters.

The monophyly of the genus *Anatherostipa* is supported by all our molecular analyses (Figs. 1–3) and *Ptilagrostis* appears to be the sister group of *Anatherostipa* plus *Piptochaetium* (Figs. 2 & 3). Key features of *Anatherostipa* other than the "saw" like lemma epidermal pattern, are the short glumes relative to the lemmas, long (often prow-tipped) paleas, and lemmas occasionally with small teeth or lobes at the apices (Matthei 1965; Barkworth & Everett 1987). These lemma apex characteristics were considered by Tzvelev (1977) to be an ancestral or plesiomorphic state in the Stipeae. Species of *Anatherostipa* share the lemma surface pattern and apical teeth character with *Ptilagrostis*.

The great variation in morphological forms, particularly the diversity of modifications in shape and size of floret and awn indumentum with apparent adaptive functions, within the basal lineages and MAC, is a primary reason why these separate groups were difficult to detect based solely on the study of mor-

phology. This confirms the suggestions of Thomasson (1978, 1985) and Barkworth and Everett (1987) that similar adaptive forms evolved independently, possibly synchronously under similar ecological pressures, in phylogenetically distant groups of Stipeae. Despite being morphologically diverse due to the anemochoric or herbivoric adaptations, in addition to sharing the unique lemma epidermal pattern, the basal lineages among themselves have relatively low levels of divergence in DNA sequences. The divergence value for the most variable ITS region was 17.6% for the out-group to ingroup taxa and is only 2.9% for the basal lineages. This latter value is not significantly higher than for *Nassella* where it was 2.6%. Relatively high (up to 4%) sequence divergence values between the basal lineages and the *Hesperostipa* clade indicates a greater evolutionary distance between them even though they share the "saw" like lemma pattern. The "saw" like lemma epidermal pattern found in the basal lineages is also known to occur in *Hesperostipa* (Thomasson 1978, 1980, 1982, 1985; Barkworth 1990; Cialdella & Giussani 2002). *Hesperostipa* also shares a long and prow-tipped palea with *Anatherostipa* (Barkworth & Everett 1987). *Hesperostipa* is a small phylogenetically and geographically isolated genus of the North American Stipeae.

Pappostipa.—The phylogenetic history of the *Pappostipa* clade supported by our molecular analysis of plastid DNA and nrDNA sequences (Figs. 1–3) provides evidence that *Jarava* s.l. is polyphyletic and the circumscription of the genus proposed by Peñailillo (2002) cannot be maintained. Consequently, we elevated all of Spegazzini's *Stipa* sect. *Pappostipa* to generic status based on corroborating morphological and anatomical evidence of differences with the remainder of *Jarava*. The phylogenetic resolution of *Austrostipa* and *Achnatherum* clades between *Pappostipa* clade and more highly derived *Jarava* s.s. clade clearly indicates that *Pappostipa* and *Jarava* s.s. do not share a most recent common ancestor. *Pappostipa* appears to be independently derived from the group we have called the Major American Clade (MAC). MAC is comprised of related genera that are geographically restricted to the Americas, with *Jarava* s.s. and *Nassella* constituting the principal part of the clade. Recent phylogenetic inferences based on plastid DNA sequences for the South American Stipeae (Cialdella et al. 2007) revealed the affinities of *Pappostipa* with the basal lineages since *Pappostipa vaginata* was inferred to be the sister group of an *Aciachne-Anatherostipa-Piptochaetium* clade. The phylogenetic position of *Pappostipa speciosa* (reported as "*Achnatherum speciosum*") within the *Achnatherum* clade based on ITS sequences by Jacobs et al. (2000, 2007) is refuted by our more extensive analysis.

Some key morphological features of the *Pappostipa* floret indicate transitional characteristics leading to the more advanced states found in MAC, or to analogous states of characteristics independently derived in other genera. Unigeniculate awns, straight and long-hairy columns, and usually straight glabrous bristles are the principal diagnostic characters for *Pappostipa* (Spegazzini 1901). The same suite of morphological features of the awn is developed in central Asian *Stipa* sect. *Pseudoptilagrostis* Tzvel. (Tzvelev 1977) and two Mediterranean genera, *Celtica* F.M. Vázquez & Barkworth and *Macrochloa* Kunth (Vázquez & Barkworth 2004). Among awn characteristics, *Ptilagrostis* differs from *Pappostipa* by having twice geniculate awns, and *Macrochloa* differs from *Pappostipa* by having falcate rather than straight bristles. The callus of *Pappostipa* is narrowly acute to acuminate with a characteristic lanceolate or linear-lanceolate form with a basally open foveola that follows the shape of the peripheral ring (Fig. 4A–C). However, a similar structure is known in *Stipa subsessiliflora* (Rupr.) Roshev. and *Stipa* sect. *Pseudoptilagrostis* (Freitag 1985; Barkworth & Everett 1987. After complete removal of the cuticle the walls of the lemma epidermal cells appear to be sinuate in *Pappostipa* (Fig. 4G) and not lobate. This type of lemma epidermal wall can be considered transitional between the "saw" like pattern found in *Hesperostipa* and other basal lineage genera (Fig. 4G) and the pattern found in MAC. However, the moderate shortening of the fundamental cells and their regular alternating pattern with equilateral silica cells ("maize" like pattern) enables us to associate the lemmas of *Pappostipa* with other achnatheroid type species rather than with the pattern encountered in the basal lineages.

Our ITS analysis and combined plastid DNA and nrDNA analyses (Figs. 2&3) divides *Pappostipa* into two clades that are correlated with anatomical types I & II of Arriaga (1983). These lineages are here named as *Pappostipa* sect. *Pappostipa* and *P.* sect. *Chysovaginatae*. Based on our molecular analyses and by possessing a suite of anatomical and leaf morphological characteristics we placed *Pappostipa barrancaensis, P. braun-*

blanquetii, P. hieronymusii, P. maeviae, P. major, P. malahuensis, P. nicorae, P. parodiana, P. patagonica, P. ruiz-lealii, P. speciosa, P. vaginata, and *P. vatroensis* in *P.* sect. *Pappostipa*; and include *P. ameghinoi, P. atacamensis, P. chrysophylla, P. chubutensis, P. frigida, P. humilis, P. ibarii*, and *P. nana* in *P.* sect. *Chysovaginatae*. Within *P.* sect. *Pappostipa* we also recognize an informal "long-bristle" group that includes *P. barrancancaensis, P. major, P. malahuensis*, and *P. vatroensis*. These four species all have long straight bristles, whereas the other species have "short bristles." We have recognized *P. speciosa* var. *major* as a species, *P. major*, based on different chromosome number reports (2*n*=60 in *P. major*; 2*n*=66 in *P. speciosa*; Parodi 1960; Stebbins & Löve 1941; Covas & Bocklet 1945), distinct differences in the length of the hairs on the lemma and glumes, thickness of the basal leaf blades, and color of the sheaths.

***Austrostipa*.**—The monophyly of the Australian Stipeae, i.e., *Austrostipa* was supported in all of our separate and combined analyses of plastid DNA and nrDNA regions (Figs 1–3). The *Austrostipa* clade is clearly positioned as a sister group to the Major American Clade (MAC) composed of *Achnatherum, Jarava* s.s., and *Nassella* (with *Amelichloa* nested inside). This general relationship, but with more Asian genera represented in the clade in which *Austrostipa* was included, was detected by Romaschenko et al. 2007. The monophyly of the *Austrostipa* was supported by Jacobs et al. (2000, 2007) based on the ITS analysis. However, the clade was thought to be the most derived group in the Stipeae, preceded by clades or grades containing *Nassella, Jarava*, and *Achnatherum*. It has been pointed out by Barkworth and Everett (1987) that the majority of the *Austrostipa* species do not have shortened fundamental cells, which is a distinctive character in species of *Nassella* and *Jarava* s.s. In addition, it was found that *Austrostipa* species typically have fundamental cells with slightly sinuate walls that sometimes are two or three times longer than the silica cells (Jacobs & Everett 1996). Therefore, we consider *Austrostipa* to be a somewhat specialized group and transitional to the American *Achnatherum*. However, the nature of this lineage will be covered in more detail in a separate paper where it will be placed in context of a World wide sample of the Stipeae.

***Major American Clade*.**—One of the primary challenges of this study was to verify monophyly and ascertain the boundaries of the largest group of American Stipeae. We call it the Major American Clade (MAC) because it contains nearly 72% of the species in the American Stipeae. MAC appears to be monophyletic and is a geographically distinct lineage comprised of *Achnatherum* (American lineage), *Jarava* s.s. (as a clade or grade), *Amelichloa*, and *Nassella*. MAC has consistent statistical support (Figs. 1–3) as a lineage and appears as a sister group to *Austrostipa*. The detection of MAC provides a new phylogenetic hypothesis for the evolutionary derivation of the majority of the American Stipeae.

***Achnatherum*.**—The monophyly of the subset American species of *Achnatherum* sampled (4 out of 34 species) was supported by our plastid and nuclear-derived trees (Figs. 1–3) and this *Achnatherum* clade was always the sister group to the *Jarava* s.s. plus the *Nassella-Amelichloa* complex, in agreement with analyses by Jacobs et al. (2000). Jacobs et al. (2000) suggested that *Achnatherum* was a close relative of *Austrostipa*, a hypothesis that is also supported by our analysis. *Achnatherum* clearly exhibits a derived lemma epidermal pattern (with fundamental cells that alternate with silica cells forming a clear "maize" pattern), and does not have the "saw" like lemma epidermal pattern found in the basal lineages and *Hesperostipa*.

***Jarava s.s-Nassella complex*.**—The core of MAC is the *Jarava* s.s. plus *Nassella-Amelichloa* complex. This group contains ca. 160 species, representing about 60% of the American Stipeae. In all combined analyses of plastid DNA and nrDNA this clade was resolved as monophyletic with high statistical support (Figs. 1–3). Jacobs et al. (2000, 2007) did not detect this complex as a clade in their ITS tree, whereas recent phylogenetic inferences based on plastid DNA data (Cialdella et al. 2007) are consistent with our results. However, topologies yielded by parsimony and Bayesian analyses were not consistent when using separate data sets of plastid and nuclear markers. Based on combined data of plastid DNA regions, *Jarava plumosula* was placed in a polytomy between the *Nassella-Amelichloa* clade and the core of *Jarava* s.s. clade. *Jarava* s.s was resolved as monophyletic only in combined analysis of all genetic markers (Fig. 3).

Morphologically, the *Jarava* s.s. plus *Nassella-Amelichloa* complex exhibits short paleas and short funda-

mental cells. These traits are most highly developed in *Nassella* where species are characterized by having a "ladder" pattern of the lemma epidermal cells, designated by Barkworth (1990) as the "nasselloid type" (short, silicified fundamental cells not alternating with silica cells, or fundamental cells and short cells that lack silica) that are indistinguishable from each other. Another distinct feature of species with nasselloid type lemma anatomy is the development of the crown (a fleshy, ciliate formation) at the apex of the lemma. Species of *Jarava* s.s. are characterized here as the "achnatheroid type," with fundamental cells that alternate with silica cells of the same form (Fig. 4H), forming a clear "maize" pattern, and with the absence of a lemma crown. Among other achnatheroid traits common for *Jarava* s.s. species, but not observed in *Nassella* or *Amelichloa*, are the protruding and/or in some cases reduced, lemma lobes.

***Jarava* s.s.**—Based on our current set of samples, as seen in Figs. 2&3, the *Jarava* s.s. clade consists of two distinct groups: 1) *Jarava ichu* group; and 2) *J. plumosula* group. In the ITS analysis, the *Jarava* s.s. clade was resolved to be polyphyletic, with three species constituting *J. plumosula* group forming a clade that is sister group to *Nassella-Amelichloa* (Fig. 2). In the plastid analysis (Fig. 1) only *J. plumosula* resolved in a polytomy between the core of *Jarava* and *Nassella-Amelichloa*, whereas *J. media* and *J. polyclada* were placed just at the base of the clade of *Jarava* s.s. (core) plus *Nassella-Ameichloa* complex. In the analysis of the whole molecular dataset, all species of *Jarava* s.s. were weakly supported as monophyletic clade (Fig. 3). *Jarava media, J. plumosula*, and *J. polyclada* all share the same habitat and a habit that includes such characters as culms having many branches at the upper nodes, and a zoo-anemochoric floret dispersal adaptations.

Our combined plastid and ITS molecular analysis (Fig. 3) supports the separation of *Jarava leptostachya* from species formerly recognized as *Stipa capilliseta* Hitchc. [≡ *S. leptostachya* var. *capilliseta* (Hitchc.) Parodi, currently treated as a synonym of *J. leptostachya* in Soreng et al. 2003] and consequently, labeled on the trees as *J. leptostachya*[2]. This separation is supported by morphological differences such as, a flexuous awn and sparsely hairy lemma apices in *S. capilliseta* verses a geniculate awn and pappose lemma apices in *J. leptostachya*.

***Nassella* including *Amelichloa*.**—According to the latest revision, *Nassella* is one of the largest genera in the tribe (Barkworth & Torres 2001) with some 119 species listed as accepted by Soreng et al. (2003). A number of subgeneric and sectional names were employed in *Stipa* s.l. by Spegazzini (1901, 1925) and Roig (1964) to recognize the many forms now placed in *Nassella*. Despite some striking morphological differences among the species, the majority of the species of *Nassella* share the same "nasselloid" pattern of the floret defined by Barkworth (1990). This pattern includes short paleas, strongly overlapping lemma margins, presence of crown, and a unique lemma epidermal pattern. Our nuclear and combined plastid-nuclear consensus trees yielded a *Nassella-Amelichloa* clade with high statistical support (Figs 2 & 3). The internal structure within our *Nassella-Amelichloa* clade is represented by two well-supported branches accommodating groups of species of varying morphological homogeneity. Within *Nassella*, the upper clade of Figs. 2 & 3 (incl. *N. brachychaetoides, N. brachyphylla, N. caespitosa, N. dasycarpa, N. depauperata, N. inconspicua, N. meyeniana, N. nardoides, N. pubiflora*, and *N. rupestris*) shares similar morphological features as described for *Stipa* subg. *Dasystipa* Speg. by Spegazzini (1901). This group typically has: oblong or lanceolate, often truncate florets, hairy lemmas (sometimes the hairs are much longer at the apex of the lemma), eccentric marginiform crowns (rarely inconspicuous), and florets with a short callus. The lower clade within *Nassella* (Figs. 2&3) includes *Amelichloa* (*A. caudata* and *A. clandestina*) and taxa attributed to *Stipa* subg. *Stephanostipa* Speg. (incl. *N. clarazii, N. filiculmis, N. manicata, N. neesiana, N. nidulans, N. pfisteri*, and *N. rosengurttii*), *Stipa* subg. *Nassella* (*N. trichotoma, N. tenuissima and N. sanluisensis* sensu Spegazzini 1901), and *Stipa* subg. *Microstipa* (incl. *N. filiculmis* sensu Spegazzini 1901; and *N. tenuissima* sensu Roig 1964). In combined plastid DNA-nrDNA and ITS analyses the *Amelichloa* subclade was resolved as monophyletic (PP=1.00; BF=100) as a sister group to the lower clade of *Nassella*. The position of the *Amelichloa* clade near the base of this lower *Nassella* clade was unexpected. However, all species of *Nassella-Amelichloa* share a deletion of three nucleotides at the end of the ITS-2 region (not coded for this analysis) not found in other taxa of our analysis. The position of *Amelichloa* within *Nassella* requires study of additional species prior to proposing taxonomic changes.

CONCLUSIONS

Jarava s.l. is polyphyletic and species formerly in *Stipa* subg. *Pappostippa* are removed from *Jarava* s.l. and placed in the new genus *Pappostipa*. This new genus is phylogenetically intermediate between a group of genera designated as the basal lineages in the American Stipeae and a set of genera designated here as the Major American Clade. The Major American Clade includes: *Achnatherum* of the New World, *Jarava* s.s., and *Nassella* (in which the genus *Amelichloa* is phylogenetically nested). The American basal lineages include a clade of *Anatherostipa* and *Piptochaetium* as sister group to the Asian and American genus *Ptilagrostis*. Phylogenetically, the North American genus *Hesperostipa* stands between these American basal lineages and *Pappostipa* plus the Major American Clade.

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INFRAGENERIC CLASSIFICATION AND NOMENCLATURAL NOTES FOR *PYCNANTHEMUM* (LAMIACEAE)

Kenton L. Chambers and Henrietta L. Chambers

Department of Botany and Plant Pathology
Oregon State University
Corvallis, Oregon 97331, U.S.A.

ABSTRACT

The history of sectional classifications of *Pycnanthemum* is discussed, and it is proposed to modify the infrageneric arrangement by Bentham (1848) to account for more recent biosystematic studies of the genus. Seven sections are proposed: 1. Sect. *Pycnanthemum,* 2. Sect. *Aristatae,* 3. Sect. *Brachystemum,* 4. Sect. *Capitellatae,* 5. Sect. *Macrocephalae,* 6. Sect. *Nudae,* and 7. Sect. **Californicae**. Each section is based on one diploid species (except 3 in Sect. 1) and may include one or more derived allopolyploid species that most resemble(s) the diploid progenitor(s). Similarities used for sectional assignment of the alloploids are chiefly key features of leaf shape, habit, inflorescence morphology, and chromosome number. Published chromosome counts and hybridization studies have shown the genus to be a hybrid, polyploid, and partly agamospermous complex. Taxa of hybrid origin link the basic diploid species of different sections. The placement of the derived, principally tetraploid, species in one or another parental section involves arbitrary decisions based on the key traits mentioned above. In a reticulate genetic complex such as this, the ideal of a classification with only monophyletic categories is not possible. Our sections are based on the diploid entities that resulted from early divergent evolution in the genus, while the later-formed hybrid and morphologically intermediate taxa are accommodated in the most practical way possible. Lectotypes are designated for the sections proposed by Bentham (1848) and for *Satureja virginiana* L., the basionym of *Pycnanthemum virginianum* (L.) Robins. & Fernald.

RESUMEN

Se discute la historia de las clasificaciones seccionales de *Pycnanthemum,* y se propone modificar la ordenación infragenérica de Bentham (1848) para explicar los estudios biosistemáticos más recientes del género. Se proponen siete secciones: 1. Sect. *Pycnanthemum,* 2. Sect. *Aristatae,* 3. Sect. *Brachystemum,* 4. Sect. *Capitellatae,* 5. Sect. *Macrocephalae,* 6. Sect. *Nudae,* y 7. Sect. **Californicae**. Cada sección está basada en una especie diploide (excepto 3 en la Sect. 1) y puede incluir una o más especies derivadas alopoliploides que más se parezcan al progenitor diploide. Las similitudes usadas para la asignación seccional de los aloploides son principalmente características de la forma de la hoja, hábito, morfología de la inflorescencia, y número cromosomático. Los recuentos cromosomáticos publicados y los estudios de hibridación han demostrado que el género es un complejo híbrido, poliploide y parcialmente agamospermo. Los taxa de origen híbrido unen las especies básicas diploides de diferentes secciones. La colocación de las especies derivadas, principalmente tetraploides, en la sección de uno u otro parental implica decisiones arbitrarias basadas en los caracteres clave mencionados más arriba. En un complejo genético reticulado como este, el ideal de una clasificación que sólo tenga categorías monofiléticas no es posible. Nuestras secciones se basan en entidades diploides que resultaron de una evolución divergente temprana del género, mientras que los híbridos formados más tarde y taxa morfológicamente intermedios se acomodan del modo más práctico posible. Se designan lectotipos para las secciones propuestas por Bentham (1848) y para *Satureja virginiana* L., el basiónimo de *Pycnanthemum virginianum* (L.) Robins. & Fernald.

A PROPOSED SECTIONAL ARRANGEMENT OF *PYCNANTHEMUM* SPECIES

Up to the time of George Bentham's treatment of *Pycnanthemum* for the *Prodromus* of Alphonse de Candolle (1848), two principal species-groups had commonly been recognized, first as the two genera *Pycnanthemum* and *Brachystemum* by Michaux (1803) and then as Section *Tullia* and Section *Brachystemum* by Bentham (1834). In his more elaborate treatment of 1848, Bentham formally described six sections, to be discussed below. The much later generic monograph by Grant and Epling (1943) did not recognize formal sections, but rather defined two principal groups, termed the Incanum Phylad, of 8 taxa, and the Virginianum Phylad, of 5 taxa. The remaining 8 species were irregularly connected to these groups in a chart (their Figure 1) displaying a network of relationships and suggesting multiple transitional forms and gene exchange between taxa. In their analysis, only *P. californicum* and *P. nudum* "present no transitional forms with other species."

In our previous papers and unpublished work (Chambers 1961a, b; Chambers & Chambers 1971; Chambers 1993) no formal sections of *Pycnanthemum* were recognized, but the taxa were arranged in six informal "species groups." These paralleled the named sections of Bentham but differed in some respects, due

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to the addition of several species to the genus after his publication, as well as new information gained from our cytological and hybridization studies. We went beyond Grant and Epling (1943) in not only recognizing their "Incanum" and "Virginianum" phylads, but also in organizing the outlying taxa of their relationship network into arbitrary species groups. Our informal classification is given in Table 1, which lists the known somatic chromosome numbers of each species (Chambers & Chambers 1971).

While Grant and Epling (1943) spoke of transitional forms between species and the possibility that some species were themselves of hybrid origin, our later work (Chambers 1961a, b; Chambers & Chambers 1971, Chambers 1993) has defined the genus as a polyploid complex, with 9 extant diploid species (Table 1), apparent autopolyploidy in *P. albescens*, *P. muticum*, and *P. tenuifolium*, and 10 taxa that are limited to the tetraploid level. The latter appear, for the most part, to be morphologically intermediate between known diploids, such that an alloploid origin is strongly suggested. Accompanying this polyploid evolution in some species has been the development of facultative or obligate agamospermy, marked morphologically by flowers with short filaments and aborted anthers. Where tested in sterile-anthered plants of *P. virginianum*, *P. verticillatum*, and polyploid *P. muticum*, seed-set was normal in both bagged and un-bagged inflorescences (Chambers 1961). Plants with aborted anthers also occur in *P. tenuifolium*, but although apomictic behavior is suspected, it has not yet been checked experimentally (Chambers 1961).

Although it would be desirable to divide the genus entirely into monophyletic sections, we believe that the reticulate nature of evolution in *Pycnanthemum*, involving, as it does, allopolyploidy, a polyphyletic hybrid origin[1] for several widespread taxa, and the preservation of sterile hybrids via apomixis, precludes such a classification at present. Our approach is to propose a practical infrageneric classification involving certain arbitrary decisions about the placement of species that putatively are derived from allopolyploidy or complex polyphyletic hybridity. Basic to our classification is that each section contains one or more of the known sexual diploid species, and no sections are composed only of polyploids (alloploids, complex hybrids, or apomicts). By this plan, we have chosen to place each taxon of suspected hybrid origin into whichever section contains the diploid(s) it most resembles morphologically. This has involved a choice of emphasis on certain key features, especially those of habit, leaf morphology, and details of the inflorescence. An example of this decision process is discussed under *P. setosum*, below.[2]

Complementing the chromosomal and hybridization research mentioned above have been two recent studies using molecular approaches. The thesis by Yetter (1989) examined relationships in the Virginianum Group, using 12 enzyme systems to identify synapomorphic alleles as well as alleles unique to particular diploid taxa. The work of Williams (2005) developed a cladogram of relationships among all but one species of *Pycnanthemum*, based on sequence data from the ITS region of nuclear ribosomal DNA. (Technical difficulties prevented the inclusion of *P. setosum*. Nominally no *P. clinopodioides* was included in her study, but it may have been represented by a population that she classified as *P. torreyi*)

Our proposed sectional classification takes account of the molecular information from the above research. It emphasizes the nine basic diploid species, using morphological evidence to place each allopolyploid taxon arbitrarily in association with the parent species that it more resembles. The named sections and their included species are presented below, with diploid species in bold-face.

1. Sect. Pycnanthemum. Type: *Clinopodium incanum* L., typ. cons. = *P. incanum* (L.) Michx.

Syn.: Sect. *Tulliae* Benth. in DC. Prod. 12:187. 1848. Type: *Tullia pycnanthemoides* Leavenw. (lectotype, designated here, Amer. J. Sci. Arts, Ser. 1, 20:343, t. 5, 1831, = *P. pycnanthemoides* (Leavenw.) Fernald).

Included species.—***P. albescens*** Torr. & A. Gray, ***P. curvipes*** (Greene) E. Grant & Epling, ***P. loomisii*** Nutt., *P. clinopodioides* Torr. & A. Gray, *P. incanum* (L.) Michx., *P. pycnanthemoides* (Leavenw.) Fernald.

[1]A hypothesized origin through numerous, independent hybridization events between different populations of the putative ancestral species.

[2]Dr. P.D. Cantino has made the interesting suggestion (pers. comm.) that the problem of classification of hybrids through arbitrary assignment to formal sections might be avoided through the use of PhyloCode nomenclature. In our opinion, a much better developed morphological and molecular cladistic phylogeny for *Pycnanthemum* is needed, before applying PhyloCode methods to the monophyletic groups hypothesized in our studies.

Table 1. Informal species groups used in the papers by Chambers and Chambers. Diploid numbers and names of species that are partly or wholly diploid are in bold-face.

Species Group	Included species	Chromosome numbers (2n)
Incanum Group	***P. albescens***	**38**, 76
	P. loomisii	**38**
	P. curvipes	**40**
	P. pycnanthemoides	72
	P. incanum	76*
	P. clinopodioides	76
	P. floridanum	78
Flexuosum Group	***P. flexuosum***	**36**
	P. setosum	76
Virginianum Group	***P. muticum***	**40**, 80, ca. 108
	P. tenuifolium	**40**, 80
	P. pilosum	78
	P. torreyi	80
	P. verticillatum	ca. 76–78
	P. virginianum	80
Montanum Group	***P. montanum***	**40**
	P. beadlei	76
Nudum Group	***P. nudum***	**40**
Californicum Group	*P. californicum*	**40**

* The reported count of 2n=78 for *P. incanum* (Chambers 1993) was a misprint for 2n=76.

2. Sect. Aristatae Benth. in DC. Prod. 12:186. 1848. Type: *P. aristatum* Michx. (lectotype, designated here, Fl. bor.-amer. 2:8, pl. 33, 1803, = *P. setosum* Nutt.).

Included species.—***P. flexuosum*** (Walt.) Britton, Sterns & Poggenb. (syn.: *P. hyssopifolium* Benth.), *P. setosum* Nutt.

3. Sect. Brachystemum (Michx.) Benth., Labiat. gen. spec. 329. 1834. Type: *Brachystemum muticum* Michx. (lectotype, effectively designated by Grant & Epling, Univ. Calif. Publ. Bot. 20:202. 1943), = *P. muticum* (Michx.) Pers.).

Syn.: Sect. *Mutica* Benth. in DC. Prod. 12:188. 1848. Type: *Brachystemum muticum* Michx. (lectotype, designated here, Fl. bor.-amer. 2:6, pl. 32. 1803, = *P. muticum* (Michx.) Pers.).

Included species.—***P. muticum*** (Michx.) Pers., *P. beadlei* (Small) Fernald, *P. floridanum* E. Grant & Epling.

4. Sect. Capitellatae Benth. in DC. Prod. 12:189. 1848 (as *Capitellata*). Type: *Brachystemum lanceolatum* Willd. (lectotype, designated here, Willdenow, Enum. pl. 623.1809, = *P. virginianum* (L.) Robins. & Fernald).

Included species.—***P. tenuifolium*** Schrad., *P. pilosum* Nutt., *P. torreyi* Benth., *P. verticillatum* (Michx.) Pers., *P. virginianum* (L.) Robins. & Fernald.

5. Sect. Macrocephalae Benth. in DC. Prod. 12:189. 1848 (as "*Macrocephala*"). Type: *P. montanum* Michx.

Included species.—***P. montanum*** Michx.

6. Sect. Nudae Benth. in DC. Prod. 12:189. 1848 (as "*Nuda*"). Type: *P. nudum* Nutt.

Included species.—***P. nudum*** Nutt.

7. Sect. Californicae K.L. Chambers & H.L. Chambers, sect. nov. Type: *P. californicum* Durand, J. Acad. Nat. Sci. Philadelphia Ser. II, 3:99. 1855.

Plantae superne albo-tomentosae foliis subsessilibus cordatis vel truncatis ovatis acutis denticulatis floribus capitatis terminalibus et in axillis bractearum dispositis bracteis foliaceis bracteolis capitulorum erectis angustis calicibus equidentatis dentibus triangulatis dense tomentosis corollis maculatis staminibus exsertis.

Included species.—***P. californicum*** Durand.

Lectotypes are proposed, above, for the sections of Bentham containing more than one species. As noted, the genus *Brachystemum* was earlier typified by Grant and Epling (1943) with *B. muticum*, so Bentham's Section *Mutica* becomes superfluous. For Sect. *Capitellatae*, of the two species cited by Bentham we have elected Willdenow's (1809) *B. lanceolatum* (= *P. virginianum*) as the type rather than his *B. linifolium* (= *P. tenuifolium*), because the latter name is illegitimate, and Willdenow's description is at variance with the type and description of *Satureja virginiana* L., the origin of his cited synonym *Thymus virginicus* L. (1771).

Section *Pycnanthemum* is the only section containing more than one diploid species. Its members are characterized by loose, well-branched flower clusters, both terminal and (often) in the axils of 1–4 bracteate leaf pairs below this. Leaves are broad, petiolate, and often canescent on one or both sides, especially distally on the plant. We hypothesize that this section contributed to the origin of intersectional alloploids showing a tendency toward relatively tight but visibly branched flower clusters, for example *P. beadlei*, *P. floridanum*, and *P. pilosum*, the other putative parents having tight capitula.

We follow Bentham (1848) in placing *P. flexuosum* in Sect. *Aristatae*, in association with its very likely allotetraploid derivative *P. setosum* (see chromosome pairing of 19 IIs and 18 Is at meiosis in triploid backcross hybrid #75, Chambers 1993). The other putative parent of *P. setosum*, *P. muticum*, is in Sect. *Brachystemum*. An alternative would be to create a monotypic section for *P. flexuosum* and leave *P. setosum* alone in an alloploid Sect. *Aristatae*, but this goes against our plan to have each section contain at least one diploid species. Additionally, it would create a precedent for other alloploid species like *P. floridanum*, *P. beadlei*, *P. virginianum*, et al., to be segregated into monotypic sections of their own. The resemblance of *P. setosum* to *P. flexuosum* is expressed in features of stem puberulence, distinct branchlets in the capitula, aristate inflorescence bractlets, reduced calyx pubescence, and calyx teeth acuminate with an aristate tip up to 1 mm long. Especially in the northern portion of its range, *P. setosum* often resembles its other putative parent *P. muticum* in traits of habit (general absence of leafy, sterile side-branches), leaf shape (more broadly lanceolate leaves), and upper bracteate leaf pair subtending the capitula (reduced, ovate, canescent, and often drooping). Besides its morphological intermediacy, *P. setosum* has 2n=76, which is the sum of the diploid numbers of the putative parental species.

Section *Brachystemum*, centered on diploid *P. muticum*, also provides other examples of alloploid species being included, by choice, with one of their likely diploid ancestors. A relationship of tetraploid *P. floridanum* to *P. muticum*, as is suggested by the DNA data of Williams (2005), implies that the gametic number n=39 in *P. floridanum* must include a 20-chromosome genome derived from *P. muticum*. On morphological and cytological grounds, *P. floridanum*'s other diploid parent is probably a species with n=19 in Sect. *Pycnanthemum* (as predicted by Grant and Epling 1943, p. 210, referring to their Incanum Phylad). One candidate taxon is *P. albescens*, but this possible relationship has not yet been tested experimentally. In a further example, *P. beadlei*, another tetraploid, has traditionally been associated taxonomically with *P. montanum* (they are sympatric in the southern Appalachians). However, Williams' DNA data from nuclear ribosomal ITS genes (2005) do not support a close phylogenetic relationship between the two. Instead, *P. beadlei* appears in a clade with *P. muticum* and some of its other tetraploid derivates. The chromosome numbers of n=38 in the former species and n=20 in the latter suggest that a second genome of 18 occurs in *P. beadlei*, perhaps from an ancestral diploid in Sect. *Pycnanthemum*, where x=18 is known (although no extant species have n=18). Artificial hybrids #12 and #15 between *P. beadlei* and *P. muticum* (Chambers 1993) showed up to 20 chromosome pairs and 18 singles at first division of meiosis in pollen-mother cells. *Pycnanthemum beadlei* is therefore assigned to Sect. *Brachystemum*.

Section *Capitellatae* contains the core of the earlier Virginianum Complex, which we view as comprising *P. tenuifolium* plus hybrid derivatives of that taxon with members of one or more other sections. *Pycnanthemum tenuifolium* is distinguished by its linear leaves, numerous small and compact floral heads, bractlets of the heads acuminate, pungent, and arcuate basally, with stout, emergent midnerve, and a bushy habit due to numerous vegetative branches arising from the stem nodes. In the derived tetraploid species *P. virginianum*, *P. pilosum*, *P. torreyi* and *P. verticillatum*, the leaves are usually lanceolate, the heads somewhat looser (espe-

cially *P. pilosum*), the capitular bractlets less pungent (though still with a notably stout midnerve), and the habit frequently less bushy. There is good molecular evidence that the broader leaves, less-branched habit, and non-pungent bractlets came from the second parent of many tetraploid forms, namely *P. muticum* (Yetter 1989; Williams 2005). From his allozyme studies, Yetter concluded: "Tetraploids traditionally labeled *Pycnanthemum virginianum* and *P. pilosum* are thought to be allopolyploid derivatives of diploid *P. muticum* and *P. tenuifolium* as indicated by the possession of alleles which are unique to the diploids" (1989, p. 80). In the DNA analyses by Williams (2005), samples of the alloploid taxa *P. virginianum*, *P. pilosum*, and *P. verticillatum*, of Sect. *Capitellatae*, were always associated in her cladograms with *P. tenuifolium* or *P. muticum*, not with species from other sections. Additional evidence comes from the artificial diploid hybrid of *P. muticum* × *P. tenuifolium* (#84, Chambers 1993). In the morphology of habit, leaves, and floral capitula, this hybrid can easily be classified as *P. virginianum* (voucher OSC 192224). Our assignment of *P. muticum* to the separate Sect. *Brachystemum* recognizes its involvement in other intersectional hybrids in addition to those involving *P. tenuifolium*. Finally, we differ from Bentham (1848) in placing *P. torreyi* in the same section as *P. tenuifolium* rather than with *P. muticum*, but this is tentative awaiting further study, since DNA evidence suggests that *P. torreyi* is itself of complex, polyphyletic hybrid origin (Williams 2005).

The monotypic sections *Macrocephalae*, *Nudae*, and *Californicae* are not at this point implicated in the origin of any polyploid taxa. However, intersectional hybrids have been produced artificially (Chambers & Chambers 1971; Chambers 1993), and a natural hybrid of *P. nudum* × *P. flexuosum* has been described (Chambers & Chambers 1971). Hybrids with mostly sterile pollen have been produced in crosses of *P. muticum* × *P. montanum*, *P. muticum* × *P. californicum*, *P. muticum* × *P. tenuifolium*, *P. flexuosum* × *P. nudum*, *P. flexuosum* × *P. tenuifolium*, and *P. flexuosum* × *P. loomisii* (Chambers 1993). Puzzling intermediate forms will no doubt be found in nature involving these and other species, such that species boundaries, especially at the tetraploid level, will be blurred (Grant & Epling 1943, pp. 233–236). Even if sterile, such hybrids may occasionally persist through seed apomixis or vegetative clonal reproduction.

Our revised sectional classification of *Pycnanthemum* is summarized in Table 2. A taxonomic treatment of the genus is in preparation for inclusion in a future volume of *Flora of North America* (Flora of North America Editorial Committee, 1993 onwards).

LECTOTYPIFICATION OF *PYCNANTHEMUM VIRGINIANUM* L.

There are three species named by Linnaeus in *Species Plantarum* (1753) that today are placed in the genus *Pycnanthemum*. These are *Satureja virginiana* (p. 567), *Nepeta virginica* (p. 571), and *Clinopodium incanum* (p. 588). *Clinopodium incanum* L., now *Pycnanthemum incanum* (L.) Michx., is the conserved type of the genus (Rickett & Stafleu 1960; McNeill et al. 2006). It was lectotypified with a Kalm specimen, Herb. Linn. No. 742.4, by Reveal et al. (1987, see Jarvis 2007, p. 428). We would not hazard a guess as to why Linnaeus cited "*Habitat in* Europa *boreali*" for this strictly North American species.

The name *Satureja virginiana* (Linnaeus 1753, p. 567) has since 1908 or before been treated in all North American floras as the basionym of *Pycnanthemum virginianum* (L.) Robins. & Fernald, a common and widespread taxon in eastern North America. Its lectotypification has been uncertain, in part because some of the pre-Linnaean polynomials cited in the original description are known to refer to the related species, *P. tenuifolium* Schrad. (Epling 1929; Grant & Epling 1943; Jarvis 2007). Epling (1929) at first suggested that *P. virginianum* was synonymous with *P. linifolium* (Willd.) Pursh, a synonym of *P. tenuifolium*. However, in Grant and Epling (1943) he changed his mind, saying that Linnaeus had in his herbarium a specimen of what we today know as *P. virginianum*, and because this usage "has now become well established....it seems preferable not to make another change." Epling did not formally propose the Linnaean Herbarium specimen as a lectotype, however. This specimen is Herb. Linn. 744.21. It is annotated in Linnaeus' script "Sat[ureja] 1 virginiana" and reannotated by Smith "Sp. Pl. 1. Pycnanthemum linifolium Sm. in Rees's Cyclop." It is filed as sheet number 21 under the genus *Thymus* (Savage 1945).

We have examined the excellent image of this sheet available through the Linnaean Herbarium website

Table 2. Sections of *Pycnanthemum* and their included species, as here proposed. Bold-face indicates species that are partly or wholly diploid.

Section	Species
1. Pycnanthemum	**P. albescens**
	P. clinopodioides
	P. curvipes
	P. incanum
	P. loomisii
	P. pycnanthemoides
2. Aristatae	**P. flexuosum**
	P. setosum
3. Brachystemum	P. beadlei
	P. floridanum
	P. muticum
4. Capitellatae	P. pilosum
	P. tenuifolium
	P. torreyi
	P. verticillatum
	P. virginianum
5. Macrocephalae	**P. montanum**
6. Nudae	**P. nudum**
7. Californicae	**P. californicum**

(<www.linnean.org>), and we find that it is undoubtedly a specimen of *Pycnanthemum virginianum* as that name has been applied in North America for the last 100 years. There are certain details in Linnaeus' description of *Satureja virginiana* that aptly fit this specimen but that are inappropriate for *P. tenuifolium* (the other species to which "*virginiana*," or the variant "*virginica*," have been applied). Firstly, Linnaeus described the leaves as "foliis lanceolatis," and in citing his earlier polynomial from *Hortus Cliffortianus* (Linnaeus 1737, p. 305), he changed the "foliis linearibus acuminatis" from that work to "foliis lanceolatis acuminatis," presumably better to fit the specimen he had at hand. Secondly, this specimen has tiny stamens and clearly represents the agamospermous form of *P. virginianum* which is the common type found in the Atlantic Coast states (Chambers 1961a). These non-functional stamens are well described by Linnaeus in his observation, "Stamina *in fundo corollae latent* Antheris *minimis effoetis, ut fere posset genere proprio tradi.*"[3] This differs from *P. tenuifolium*, which in this same region reproduces sexually and has exserted stamens with functional anthers (Chambers 1961a).

Therefore, based on these considerations, we here designate Herb. Linn. 744.21 (LINN) as the lectotype of *Satureja virginiana* L., Sp. Pl. 1:567. 1753.

The difficult case of the name *Nepeta virginica* L., which also lacks lectotypification, is under study by James Reveal and Charlie Jarvis (pers. comm.), and their recommendation will be published in due course. The epithet "*virginica*" is not available in *Pycnanthemum*, due to the preexisting *P. virginicum* (L.) Pers. (1806) based on *Thymus virginicus* L. (1771).

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[3]Translated by us as, "Stamens lie hidden in base of corolla Anthers very small exhausted, such as hardly ever can bequeath proper offspring."

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BOOK REVIEWS

Richard B. Primack. 2002. **Essentials of Conservation Biology: Third Edition.** (ISBN 0-87893-719-6, hbk.). Sinauer Associates, Inc., 23 Plumtree Road, Sunderland, Massachusetts 01375, U.S.A. (**Orders:** www.sinauer.com, orders@sinauer.com, 1-413-549-4300, 1-413-549-1118 fax). $69.95, 698 pp., numerous figures, graphs, images, tables, 7.25" × 9.5".

Richard B. Primack. 2006. **Essentials of Conservation Biology: Fourth Edition.** (ISBN 0-87893-720-X, hbk.). Sinauer Associates, Inc., 23 Plumtree Road, Sunderland, Massachusetts 01375, U.S.A. (**Orders:** www.sinauer.com, orders@sinauer.com, 1-413-549-4300, 1-413-549-1118 fax) $82.95, 585 pp., numerous figures, graphs, images, tables, 8.75" × 11.25".

The books, *Essentials in Conservation Biology (3rd and 4th editions)*, are each divided into 22 chapters that clearly define what is meant by conservation biology, and each use detailed images, graphs, and tables to explain current issues and applications in this fairly new field.

There are only a few minor differences in the two editions, the main one being that the author continues to update each edition by providing the reader with current information within the field. In the Third Edition, the author provides a detailed introduction to the major concepts and problems in conservation biology. This book also includes information on hotspots or areas where immediate conservation is needed due to the threats to local flora and fauna. In the Fourth Edition, the author provides several new figures to better explain how the field has evolved in 4 years time. This edition also provides a glossary and an Instructors Resource CD.

I found these books to be a very interesting and quite informative read. The author clearly describes how conservation biology is very diverse and must incorporate an array of fields to help address current conservation problems and create solutions. I enjoyed the smaller size of the Third Edition, but realized that the new and larger size of the Fourth Edition was necessary in order to include the updated figures and information. This book is ideal for any introductory courses on Conservation Biology or any person that is interested in learning more about the intricate issues addressed in this relatively newer field and their possible applications.—*Keri McNew, MS Biology, Project Manager, Botanical Research Institute of Texas, 500 East 4th Street, Fort Worth, Texas 76102-4025, U.S.A.*

Glenn Keator and Alrie Middlebrook. 2007. **Designing California Native Gardens: the Plant Community Approach to Artful, Ecological Gardens.** (ISBN 978-0-520-23978-4 hbk.; 978-0-520-25110-6 pbk.). University of California Press, 2120 Berkeley Way, Berkeley, California 94704, U.S.A. (**Orders:** www.ucpress.edu, California Princeton Fulfillment Center, 1445 Lower Ferry Rd., Ewing, NJ 08618, U.S.A., 1-609-883-1759; 1-609-883-7413 fax). $65.00 hbk., $27.50 pbk., 352 pp., 364 illustrations, 7" × 9 3/4".

This book should be an inspiration to California gardeners and landscape architects whether in planning new gardens or renovating existing ones. It is also a practical manual. Taking into consideration twelve principal plant communities, from desert to coastal plains to mountains, the authors construct gardens, some in very challenging situations, and all using native plants of their respective regions.

The plants are indicated by common and by scientific names with planting notes and special features that explain their desirability and/or difficulties in using them. In addition to the photographs of individual plants, there are suggested plans, elevated drawings, and photographs of completed gardens. The authors even give attention to retrofitting urban Los Angeles with coastal scrub plantings, including green roofs. For each of the plant communities, there is a "places to go" section which includes state parks and preserves, other scenic areas, and a few public gardens where the native plants may be observed in natural habitat.

The four appendices list sources for native plants and seeds, public gardens that feature native plants, a calendar for garden activities, and a glossary of terms.—*Joann Karges, Texas Christian University Library (retired), Fort Worth, Texas, U.S.A.*

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NOMENCLATURAL NOTES IN NORTH AMERICAN *POTENTILLA* (ROSACEAE)

Barbara Ertter

Curator of Western North American Flora
University and Jepson Herbaria
University of California
Berkeley, California 94720-2465, U.S.A.
and
Research Associate
Snake River Plains Herbarium
Boise State University
Boise, Idaho 83725-1515, U.S.A.
ertter@berkeley.edu

ABSTRACT

New Manual of Botany of the Central Rocky Mountains, by J.M. Coulter & A. Nelson (1909) is an earlier source than previously noted for *Potentilla* sections *Supinae, Concinnae, Subjugae, Niveae,* and *Multifidae.* Sections *Rubricaules* and *Leucophylleae* are also established, with the latter superseding sect. *Hippianae* (Rydb.) Ertter & Reveal. The segregates from *P. pensylvanica* sensu lato that will be used in a forthcoming volume of *Flora of North America* are briefly summarized, with **Potentilla jepsonii** Ertter established as a new name for *P. pensylvanica* var. *ovium* Jepson. The distinction and identity of *P. nivea* var. *dissecta* S. Watson and *P. concinna* var. *divisa* Rydb. are clarified. Complete lectotypifications are provided for *P. litoralis* Rydb., *P. pensylvanica* var. *ovium, P. nivea* var. *dissecta, P. concinna* var. *divisa,* and *P. pseudosericea* Rydb.

RESUMEN

New Manual of Botany of the Central Rocky Mountains, by J.M. Coulter & A. Nelson (1909) es una fuente previa a las tenidas en cuenta anteriormente para *Potentilla* secciones *Supinae, Concinnae, Subjugae, Niveae,* y *Multifidae.* Las secciones *Rubricaules* y *Leucophylleae* también se establecen, con la última desbancada sect. *Hippianae* (Rydb.) Ertter & Reveal. Los segregados de *P. pensylvanica* sensu lato que serán usados en el próximo volumen de la *Flora of North America* se resumen brevemente, con **Potentilla jepsonii** Ertter establecida como un nombre nuevo para *P. pensylvanica* var. *ovium* Jepson. Se clarifican la distinción e identidad de *P. nivea* var. *dissecta* S. Watson y *P. concinna* var. *divisa* Rydb. Se aportan lectotipificaciones para *P. litoralis* Rydb., *P. pensylvanica* var. *ovium, P. nivea* var. *dissecta, P. concinna* var. *divisa,* y *P. pseudosericea* Rydb.

For a forthcoming volume of *Flora of North America* (FNA), several nomenclatural notes, lectotypifications, and a new name are required for *Potentilla* (Rosaceae); these are provided herewith.

I. Some overlooked sectional names in *Potentilla*

Subsequent to the publication of *Potentilla* sect. *Hippianae* (Rydb.) Ertter & Reveal (2007), a previously overlooked source of validly published sectional names has been encountered that supersedes sect. *Hippianae* and several other sections, at least as far as author attribution. In the key to *Potentilla* on page 255 of *New Manual of Botany of the Central Rocky Mountains* (Coulter & Nelson 1909), Nelson adopts several of Rydberg's unranked "groups" and explicitly refers to them as sections. The nomenclatural results are as follows:

Potentilla sect. **Supinae** (Lehm.) A. Nelson in J.M. Coult. & A. Nelson, New Man. Bot. Centr. Rocky Mt. 255. 1909. Basionym: *Potentilla* series *Supinae* Lehm., Revis. Potentill. 8, 191. 1856.—Antedates Johnston's (Phytologia 57:297. 1985) effort to establish the sectional name, but still later than heterotypic *P.* sect. *Rivales* Poeverl. in Asch. & Graebn. (Syn. Mitteleur. Fl. 6(1):669. 1904).

Potentilla sect. **Concinnae** (Rydb.) A. Nelson in J.M. Coult. & A. Nelson, New Man. Bot. Centr. Rocky Mt. 255. 1909. Basionym: *Potentilla* [unranked] *Concinnae* Rydb., Bull. Torrey Bot. Club 23:431. 1896.—Antedates Johnston's (Phytologia 57:299. 1985) effort to establish the sectional name.

Potentilla sect. **Subjugae** (Rydb.) A. Nelson in J.M. Coult. & A. Nelson, New Man. Bot. Centr. Rocky Mt. 255. 1909. Basionym: *Potentilla* [unranked] *Subjugae* Rydb., Bull. Torrey Bot. Club 23:397. 1896.—Antedates Johnston's (Phytologia 57:299. 1985) effort to establish the sectional name.

Potentilla sect. **Niveae** (Rydb.) A. Nelson in J.M. Coult. & A. Nelson, New Man. Bot. Centr. Rocky Mt. 255. 1909. Basionym: *Potentilla* [unranked] *Niveae* Rydb., Bull. Torrey Bot. Club 23:301. 1896.—Antedates Juzepczuk's (Fl. SSSR 10:133. 1941) use of the name at sectional rank. *Potentilla* subtrib. *Niveae* Lehm. (Revis. Potentill. 8, 163. 1856) is an invalid name (Art. 33.9 in McNeill et al. 2006).

Potentilla sect. **Multifidae** (Rydb.) A. Nelson in J.M. Coult. & A. Nelson, New Man. Bot. Centr. Rocky Mt. 255. 1909. Basionym: *Potentilla* [unranked] *Multifidae* Rydb., Bull. Torrey Bot. Club 23:262. 1896.—Antedates Juzepczuk's (Fl. SSSR 10:113. 1941) use of the name at sectional rank, but still later than heterotypic *P.* sect. *Pensylvanicae* Poeverl. in Asch. & Graebn. (Syn. Mitteleur. Fl. 9(1):669. 1904). *Potentilla* trib. *Multifidae* Lehm. (Revis. Potentill. 4, 26. 1856) is an invalid name (Art. 33.9 in McNeill et al. 2006).

Potentilla sect. **Rubricaules** (Rydb.) A. Nelson in J.M. Coult. & A. Nelson, New Man. Bot. Centr. Rocky Mt. 255. 1909. Basionym: *Potentilla* [unranked] *Rubricaules* Rydb., Mem. Dept. Bot. Columbia Coll. 2:30. 1898.—Not previously established as a section.

Potentilla sect. **Leucophyllae** (Rydb.) A. Nelson in J.M. Coult. & A. Nelson, New Man. Bot. Centr. Rocky Mt. 255. 1909. Basionym: *Potentilla* [unranked] *Leucophyllae* Rydb., Mem. Dept. Bot. Columbia Coll. 2:31. 1898.—Antedates homotypic sect. *Hippianae* (Rydb.) Ertter & Reveal (Novon 17:317. 2007).

II. Segregates from *Potentilla pensylvanica* L. sensu lato

Several entities frequently included within a broadly defined *Potentilla pensylvanica* L. (e.g., Hitchcock & Cronquist 1961, McGregor 1986) will be recognized as distinct species in FNA. The critical nomenclature is briefly summarized here, along with a new name and a lectotypification.

Potentilla pensylvanica L., Mant. Pl. 76. 1767. Lectotypification by Fernald (1935: 288) supersedes that of Soják (1987: 298). Excluded from synonymy is *P. pensylvanica* var. *strigosa* Pursh, since the homotypic *P. strigosa* (Pursh) Tratt. has been lectotypified by Soják (1987: 293) on a Pallas specimen (BM) from Siberia, which Soják identified as the hybrid between *P. pensylvanica* and the strictly Eurasian *P. sanguisorba* Willd. In D.F.K. Schltdl.

Potentilla lasiodonta Rydb., N. Amer. Fl. 22:351. 1908. An earlier name for *P. finitima* Kohli & Packer (Canad. J. Bot. 54:714. 1976), as first noted by Soják (1994: 77).

Potentilla litoralis Rydb., Bull. Torrey Bot. Club 23:264. 1896. Type: CANADA. Prov. Quebec. Gaspe Co.: Sta. Anne des Monts, 10 Jul 1881, *J.A. Allen s.n.* (lectotype, designated here: NY 436385). In 1988, Soják annotated but did not formally publish this specimen as lectotype; his choice is herewith honored and acknowledged. Synonyms include *P. virgulata* A. Nelson (Bull. Torrey Bot. Club 27:265. 1900) and *P. pectinata* Raf., nom. illeg. (Autik. Bot.:164. 1840, non Fisch. ex Ser. in A.P. de Candolle, Prodr. 2:581. 1825). The earlier name *P. dissecta* Pursh (Fl. Amer. Sept. 1:355. 1813) is probably also a synonym but is proposed for rejection (Ertter et al. 2008) since the name has a long history of application to unrelated species. The homotypic names *P. pensylvanica* var. *glabrata* (Lehm.) S. Watson, *P. bipinnatifida* Douglas ex Hook. var. *glabrata* (Lehm.) Kohli & Packer, and *P. glabrella* Rydb. have been applied to this entity or other components of *P. pensylvanica* s.l.; however, the type of the basionym, *P. sericea* L. var. *glabrata* Lehm., belongs to the unrelated species *P. ovina* J.M. Macoun, as noted by Soják (1996: 120).

Potentilla jepsonii Ertter, **nom. nov.** Basionym: *P. pensylvanica* var. *ovium* Jepson, Fl. Calif. 2:184. 1936; *P. litoralis* var. *ovium* (Jepson) Soják, Thaiszia 16:49. 2006. The epithet "ovina" is replaced at species rank to avoid confusion with *P. ovina*, which has an overlapping range. Of the two sheets in the Jepson Herbarium of the type collection (*Jepson 7307*), JEPS 2814 is here designated the lectotype, as the sheet with more abundant material and packeted notes. This sheet has been annotated by E. Crum as type of an unpublished variety of *P. pensylvanica*, using the epithet "decumbens."

Potentilla bipinnatifida Douglas ex Hook., Fl. Bor.-Amer. 1:188. 1832. Soják (2008) is proposing to conserve *P. bipinnatifida* against two older names: *P. normalis* Bess. ex Spreng. (Syst. Veg. ed. 16, 4, Cur. Post. 199. 1827) and *P. missourica* Hornem. ex Lindl. (Bot. Reg. 17:1412. 1831).

Potentilla bimundorum Soják, Cas. Nár. Mus., Odd. Prir. 141:195. 1974. Soják (1974) described *P. bimundorum* to accommodate all New World and some Old World plants previously placed in *P. multifida* L., which as now circumscribed is confined to the Old World.

III. Lectotypifications and identities of *Potentilla nivea* var. *dissecta* and *P. concinna* var. *divisa*

Potentilla nivea var. *dissecta* S. Watson (Proc. Amer. Acad. Arts 8:559. 1873) was described on the basis of four syntypes: "in the Rocky Mts. of British America and Montana (368 Drummond; Douglas; Howard); and in the Uintas, Utah (335 Watson, in part)." When Rydberg (1896b: 431) proposed "*P. concinna divisa* n. v.," he cited *P. nivea* var. *dissecta* "at least in part" in synonymy and included the Douglas ("*Rocky Mountains*") and Howard ("*Montana*") syntypes of *P. nivea* var. *dissecta* among the specimens representing his concept of *P. concinna* var. *divisa*. The other collections cited by Rydberg were "*South Dakota:* Jenney. 1875; W.H. Forwood, 1887; P.A. Rydberg, nos. 672 and 673. 1892. *Assiniboia:* John Macoun, no. 10,468, 1895."

Rydberg's citation of *Potentilla nivea* var. *dissecta* in synonymy has led to the interpretation that the two names are nomenclatural synonyms, with the epithet *divisa* superfluous at the varietal level (e.g., Boivin 1952, Hitchcock & Cronquist 1961). This interpretation is not supported, however, by Rydberg's use of "in part" and his explicit citation of some of Watson's syntypes to the exclusion of others. Rydberg (1896b) preceded the citation of specimens with the statement that "Dr. Watson included the three first specimens [actually only two, those by Douglas and Howard] cited below in his *P. nivea dissecta*, but in every respect they are much nearer *P. concinna* than *P. nivea*." As proof that Rydberg had two distinct entities in mind, he (1896a: 303) had not only previously cited *P. nivea* var. *dissecta* in the synonymy of *P. nivea* var. *quinquefolia* Rydb., but in his subsequent 1898 monograph of North American *Potentilleae*, he cited *P. nivea* var. *dissecta* "in part" in the synonymy of both *P. nivea* var. *altaica* (Bunge) Rydb. and *P. concinna* var. *divisa*. The Drummond and Watson syntypes of *P. nivea* var. *dissecta*, which were excluded from *P. concinna* var. *divisa*, were instead listed among the specimens seen of *P. nivea* var. *altaica*, preceded by the statement that "Watson's specimens agree exactly with the figure of *P. altiaca* [sic] in Ledebour's Illustrations, and this name is the only one available . . ." (Rydberg 1898: 87). This dual citation was repeated in Rydberg's 1908 revision, in which *P. divisa* (Rydb.) Rydb. was raised to a species and *P. nipharga* Rydb. replaced *P. nivea* var. *altaica*.

With the distinction of *Potentilla nivea* var. *dissecta* and *P. concinna* var. *divisa* established, lectotypification and identity need to be determined for both entities. Rydberg's removal of the Douglas and Howard syntypes from *P. nivea* var. *dissecta* leaves only *Drummond 368* and *Watson 335* as candidates. Soják has annotated the NY sheet of *Drummond 368* as lectotype of *P. nivea* var. *dissecta*; this choice is herewith honored and formalized. The identity of the single small, one-flowered plant is unfortunately ambiguous, with no precise locality to aid identification; because of the subpalmate/subpinnate leaves and short columnar style (ca 1 mm), it is tentatively identified as *P. saximontana* Rydb.

Of the syntypes of *Potentilla concinna* var. *divisa*, first stage lectotypification has been already been effectively accomplished by Holmgren's (1997: 100) statement that Douglas's collection from the Rocky Mountains was designated lectotype by Rydberg (N. Amer. Fl. 22:330. 1908). In that Rydberg only indicated that the Rocky Mountains were the type locality, without actually citing a specific collection, Holmgren's statement serves as an inadvertent lectotypification, without designating which herbarium houses the type. This would be GH 19535, annotated as holotype by B.C. Johnston and cited as such in his (1980:165) unpublished dissertation.

Potentilla nivea L. var. **dissecta** S. Watson, Proc. Amer. Acad. Arts 8:559. 1873, not *P. dissecta* Pursh. TYPE: "Rocky Mountains of British America," *Drummond 368* (LECTOTYPE, designated here: NY!).

= *Potentilla saximontana* Rydb.

Potentilla concinna Richardson var. **divisa** Rydb., Bull. Torrey Bot. Club 23:431. 1896. TYPE: Rocky Mountains, *Douglas s.n.* (LECTOTYPE, 1st stage designated by N. Holmgren, Intermount. Fl. 3a:100. 1997; second stage designated here: GH 19535!).

= *Potentilla concinna* var. *divisa*

IV. Lectotypification of *Potentilla pseudosericea* Rydb.

Potentilla pseudosericea Rydb. (Mem. Dept. Bot. Columbia Coll. 2:98. 1898) was described on the basis of three syntypes: "*Nevada*: Shockley, No. 592, 1888. *Rocky Mountains:* Nuttall; Fremont, No. 218, 1845–7." As noted by Jepson (1936: 184), *Shockley 592* is actually from the White Mountains of Mono Co., California, not Nevada. Of the two Shockley collections in GH annotated by Rydberg as "*P. pseudosericea* n. sp.," GH 19583 is labeled in S. Watson's handwriting as originating in Esmeralda Co., Nevada, but with the caveat "I think—ticket lost." The other (GH 19584) bears an original label on which a printed "Esmeralda Co., W. Nevada" is supplanted by Shockley's handwritten "White Mts., Mono Co., Calif., Aug. 19, 1888, *W.H. Shockley 592*," confirming that the Nevada citation was indeed erroneous.

The Shockley syntype represents the species to which the name has been traditionally applied, endemic to the east-central mountains of California, and possibly Nevada (unconfirmed). In contrast, the Nuttall

and Frémont syntypes belong to an unrelated species, *P. bipinnatifida* Douglas ex Hook. Rydberg (1898) also cited Nuttall's manuscript name "Potentilla holosericea" in synonymy and subsequently (Rydberg 1908: 348) specified "Rocky Mountains" as the type locality. This led B.C. Johnston to annotate Nuttall's specimen at NY as lectotype, and to annotate Shockley's "Nevada" syntype (GH 19583) as an unpublished variety of *P. pensylvanica* honoring the collector. However, citation of a locality alone is insufficient for lectotypification (Art. 37.3, Note 2, McNeill et al. 2006), so that effective lectotypification begins with W. Jepson's (1936: 184) citation of "White Mts., Mono Co., Cal., *Shockley 592*" as type locality. To complete the process, GH 19583 is herewith formally designated the lectotype of *P. pseudosericea.*

Potentilla pseudosericea Rydb., Mem. Dept. Bot. Columbia Coll. 2:98. 1898. Type: "NEVADA. Esmeralda Co." [actually CALIFORNIA. Mono Co.: White Mountains]: 19 Aug 1888, *W.H. Shockley 592* (Lectotype, 1st stage designated by W. Jepson, Fl. Calif. 2:184; second stage designated here: GH 19583!; isolectotypes: GH 19584, JEPS, UC).

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BOOK REVIEWS

Paul Martin Brown. 2005. **Wild Orchids of Florida.** (ISBN 0-8130-2933-3, flexbound). University Press of Florida, 15 Northwest 15th Street, Gainesville, Florida 32611-2079, U.S.A. (**Orders:** www.upf.com, 1-800-226-3822, 1-800-680-1955 fax). $24.95, 409 pp., numerous line drawings, maps, color images, keys, checklist, 6.25" × 9.25".

Contents.—Foreword; Preface and Acknowledgments; List of Abbreviations and Symbols; **Part One:** Orchids and Florida (An Introduction to Orchids; Which Orchid Is It?); **Part Two:** Wild Orchids of Florida—Native and Naturalized (Native and Naturalized Species; Introduced, Escaped, and Waifs); **Part Three:** Resources and References (Checklist of Native and Naturalized Orchids of Florida; Recent Literature References for New Taxa, Combinations, and Additions to the Orchid Flora of Florida; Synonyms and Misapplied Names; Species Pairs; Some Florida Orchid Statistics; Orchid Hunting in Florida; Plant Records and County Lines; The Southeastern Atlantic and Gulf Coastal Plains; Using Luer's *Native Orchids of Florida* (1972) in the New Century: Additions, Corrections, and Comments); Glossary; Selected Bibliography; Photo Credits; Index.

This book, *Wild Orchids of Florida*, is separated into three parts that consist of an introduction to orchids with information on how to use a key, detailed species pages on native orchids of Florida, and a resources and references section.

I found this book to be a good source for any amateur or orchid expert. The author used both common and scientific names in their description of each species with an average of two pages per description. The descriptions were consistent throughout the book and included several color images of the entire plant and close-ups of the flowers to aide in orchid identification. Line drawings of each species and a distribution map were included in the author's explanation. The book's size and weight make it an ideal companion for taking out in the field or simply on a hike. I think the book was enhanced by the author's inclusion of descriptions on several species that have been introduced to Florida. The resources and references section provides a detailed checklist, information on where to look, previous and recent orchid literature, and a glossary.—*Keri McNew, MS Biology, Project Manager, Botanical Research Institute of Texas, 500 East 4th Street, Fort Worth, Texas 76102-4025, U.S.A.*

Doug Welsh. 2007. **Doug Welsh's Texas Garden Almanac.** (ISBN 1-59544-619-3, flexbound with flaps). Texas A&M University Press, 4354 TAMU, College Station, Texas 77843-4354, U.S.A. (**Orders:** www.tamu.edu/upress, 1-800-826-8911). $24.95, 492 pp., color maps and images, b/w drawings, index, 7" × 10".

Contents.—Select Plant Lists; Almanac at a Glance; Introduction; **1)** January: Heading toward Spring; **2)** February: Hints of Spring, Reminders of Winter; **3)**. March: Spring—Get Busy; **4)** April: Get Moving—Lots to Do; **5)** May: Full Steam Ahead; **6)** June: Welcome to Texas Heat; **7)** July: Dog Days of Summer; **8)** August: Hot, Hot, Hot, and Dry Too! **9)** September: Cooling Off, Maybe? **10)** October: No Need to Stop Gardening; **11)** November: Down Time, Not Exactly; **12)** December: Dreaming of Spring; Acknowledgments; Resources; Index.

Doug Welsh's Texas Garden Almanac is an easy-to-read gardening guide especially for gardening in Texas. Each monthly chapter includes major topics for important garden design and care that are related, but not exclusive to that month. Major discussion topics include: Texas lawn basics; plant problems such as pests and diseases; container gardening; vegetable, flower and herb gardening help; plants to consider for different situations and of different colors; when to plant; pruning basics and much more. Chapters also include a few pages of "timely tips," important items to consider completing that month to maintain a beautiful and healthy garden.

Doug Welsh's Texas Garden Almanac provides easy to access Texas gardening advice at your fingertips—a must-have book for Texas gardeners!—*Lee Luckeydoo, Botanical Research Institute of Texas, 500 East 4th Street, Fort Worth, Texas 76102-4025, U.S.A.*

A SYNOPSIS OF THE MEXICAN AND CENTRAL AMERICAN SPECIES OF *VACCINIUM* (ERICACEAE)

Robert L. Wilbur
Department of Biology
Duke University
Durham, North Carolina 27708, U.S.A.
rwilbur@duke.edu

James L. Luteyn
Institute of Systematic Botany
The New York Botanical Garden
Bronx, New York 10458-5126, U.S.A.
jluteyn@nybg.org

ABSTRACT

A synopsis is presented with a key to and descriptions of the 27 species of *Vaccinium* occurring in Mexico and Central America, together with their synonymy and a citation of representative specimens. Two species are described and illustrated here as new: **Vaccinium campanense** Wilbur & Luteyn and **V. chihuahuense** Wilbur & Luteyn.

RESUMEN

Se presenta una sinopsis con claves y descripciones de las 27 especies de *Vaccinium* que se encuentran en México y América Central, también se presenta su sinonimia y se citan ejemplares representativos de estas especies. Se describen y se ilustran aquí dos especies como nuevas: ***Vaccinium campanense*** Wilbur & Luteyn y ***V. chihuahuense*** Wilbur & Luteyn.

INTRODUCTION

The representatives of the genus *Vaccinium* in Mexico and Central America were most recently treated by Sleumer (1936) in a study with the deceptively modest title of "Die Arten der Gattung *Vaccinium* L. in Zentral- und Südamerika." Sleumer's account actually covered the species of both the West Indies and Mexico as well as those occurring in Central and South America. Sleumer recognized 30 species in his treatment, but of these only 12 were known from Mexico and Central America. The present synopsis includes 27 species from Mexico and Central America, which gives some indication of the rich yield resulting from the more intensive field work that has taken place within the region in the past seven decades. More than half of the Mexican and Central American species of *Vaccinium* have been described in the most recent three decades, while only four species (or about 15%) were named in the first seventy-five years of the twentieth century and nine species (or 33%) during the nineteenth century.

Perhaps something should be said about the generic concept adopted in the present study. The generic limits are very broad and inclusive like that of Sleumer (1936) in his treatments of the West Indian, Mexican, Central American, and South American members of the genus, as well as his survey of the genus *Vaccinium* (1941) throughout its total range. In the latter paper Sleumer recognized 33 sections in the genus *Vaccinium*, which clearly demonstrates the great morphological diversity that the conservative concept of *Vaccinium* s.l. accepted. As someone whose initiation into Botany was through Small's *Manual of the Southeastern Flora* (1933), the senior author was exposed to a much narrower concept of genera. In the case of vaccinoioid genera such as *Batodendron* Nutt., *Polycodium* Raf., *Herpothamnus* Small, *Oxycoccus* Hill, *Hugeria* Small, and *Cyanococcus* Rydb., they still appear to demark natural groups biologically meaningful as genera than submerged into the vast diversity of the genus *Vaccinium* s.l. However, traditional generic concepts were recently followed by the authors (Luteyn & Wilbur 2005). Molecular data is sparse at present, but it is beginning to be helpful in sorting out some of the relationships within the tribe Vaccinieae (see Kron et al. 2002). Molecular evidence available from Kron et al. (2002) and Powell and Kron (2003) strongly suggests that the genus *Vaccinium* is polyphyletic and hence unnatural; vander Kloet (2004) and Stevens et al. (2004) are also of this opinion. Kron et al. (2002) concluded, however, that a much more thorough molecular survey must be completed before any formal nomenclatural changes could be made. Their prognosis for *Vaccinium* is ominous for those who were content with the heterogenous genus of 33 or so sections. Their molecular survey so far suggests that

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"*Vaccinium* will need to be enlarged to include all species currently recognized in the tribe Vaccinieae, or to be broken up" (Kron et al. 2002). Their first alternative would seem to be biologically unsound, because the resulting "*Vaccinium*" would contain so many and biologically diverse groups as to be meaningless; so we are left with the second possibility. Fortunately, Kron et al. (2002) agreed that a vast amount of work, both morphological and molecular, needs to be done before anyone should contemplate how the diverse tribe of several hundred species might best be redistributed. It seems certain that some of those groups to be recognized may be those identified by Small and others a century or more ago. We also feel that the recognition of the Central American greenish-flowered vacciniums into the genus *Symphysia* as seen by Vander Kloet et al. (2004) is premature.

We believe that a morphologically-based and field-oriented synopsis of the genus *Vaccinium* s.l. in Mexico and Central America may prove useful as a working hypothesis as botanists strive to achieve a more natural classification. Hence, this synopsis of the Mexican and Central American *Vaccinium* is presented in the hope that a new species-oriented base line will prove to be a useful summary of what is now known about the genus *Vaccinium* in the extensive and biologically interesting region of Mexico and Central America.

The newly described taxa strongly suggest that additional collecting is still very much needed. The erroneous impression exists that most of the thousands of new species that are described as new each year are present in abundance in our herbaria and that diligent general collecting is no longer needed. The species of *Vaccinium* described in the past half century—and that genus clearly is not exceptional in this regard—certainly demonstrate that all or nearly all of the newly described species are the result of material collected since Sleumer's treatment appeared and definitely are not due to the failure of Sleumer or others to make full use of the specimens available to them. A compelling case can be made that what is still needed is a well-planned, intensive collecting campaign throughout much of the area.

VACCINIUM L.

Shrubs or rarely trees, often rhizomatous, sometimes arising from lignotubers (=burls). Leaves alternate to pseudo-opposite, deciduous or briefly persistent (i.e., barely through the first unfavorable season) or persistent and evergreen, petiolate, the blades with margin entire to (slightly) serrate, the venation pinnate or plinerved. Inflorescences terminal or axillary, racemose, corymbose, rarely paniculate, or 1–2-flowered; floral bract 1, subtending each pedicel; pedicels articulate or rarely continuous with calyx; bracteoles 2. Flowers 4–5-merous, without odor; calyx synsepalous, the tube usually cylindric to globose, the lobes rarely obsolete; corolla sympetalous, aestivation imbricate, valvate or rarely open, cylindric, urceolate, globose or campanulate, white to pink, greenish or yellowish-green; stamens 8 or 10(–12), equal, included or exserted, the filaments equal, distinct or weakly connate at base, equal to or longer or shorter than anthers, the connectives lacking disintegration tissue, spurs on filaments present or lacking, sometimes with apparently vestigial spurs, the anthers equal, lacking awns, the thecae surfaces smooth or papillate, the anther tubules 2, distinct or rarely shortly connate at base, dehiscing introrsely (sometimes obliquely), latrorsely or terminally by pores or clefts; pollen grains in tetrahedral tetrads, lacking viscin strands; ovary inferior, 4–5 (or falsely 8 or 10 by partial partitions)-locular; style included or rarely slightly exserted, glabrous, the stigma small, simple or somewhat capitate. Fruit a berry, crowned by the persistent calyx lobes and capped by the conspicuous nectariferous disc; seeds many, sometimes with mucilaginous sheath.

Vaccinium is a genus with approximately 450 species distributed in the Northern Hemisphere, Mesoamerica, the West Indies, South America, E. Africa and Madagascar, Malesia, and Pacifica. Twenty-seven species from Mexico through Panama are recognized here.

KEY TO THE MEXICAN AND CENTRAL AMERICAN SPECIES OF *VACCINIUM*

1. Calyx continuous with the pedicel (i.e., lacking a disarticulation groove); corolla open just prior to anthesis or closed.
   2. Anthers conspicuously exserted beyond the corolla tube; corolla open prior to anthesis, considerably expanding and enlarging thereafter; anther spurs present ____ **1. V. kunthianum**

2. Anthers clearly included within the corolla tube; corolla closed before anthesis; anther spurs present or lacking.
   3. Erect, terrestrial shrublet arising from a subterranean, slender, woody rhizome; anthers spurred; corolla white to pinkish, 4–6 mm long, 5-lobed; leaves minutely serrate, deciduous or briefly persistent (i.e., barely through the first unfavorable season) ______ **2. V. geminiflorum**
   3. Creeping, viney, epiphytic shrublet; anthers lacking spurs; corolla red, 7–10 mm long, 4-lobed; leaves entire, persistent, evergreen ______ **3. V. dissimile**

1. Calyx articulate with the pedicel (i.e., marked by a conspicuous disarticulation groove); corolla closed prior to anthesis.
 4. Anthers spurred; leaves serrate or indistinctly crenate-serrate.
  5. Fruit in cross-section clearly falsely 10-locular; plants of Mexico and Guatemala.
   6. Inflorescences racemose with rachises (1.5–)5–9 cm long, mostly without floral bracts or only with small, subulate, deciduous bracts; corolla 3–6 mm long, campanulate to urceolate or cylindric; leaves lanceolate to lance-oblong to ovate, 12–26 mm broad; veins on the upper surface of the leaves either not or only indistinctly elevated; nectariferous disk glabrous ______ **4. V. leucanthum**
   6. Inflorescences with flowers either solitary in axils of large, leafy floral bracts **or** in racemes with rachises (1.5–)3–6 cm long with large, leafy, persistent, floral bracts; corolla 5–7 mm long, cylindric to urceolate; leaves lanceolate to lance-elliptic, (4–)8–12(–15) mm broad; veins on the upper surface of the leaves mostly pronouncedly elevated; nectariferous disk glabrous to short-pilose ______ **5. V. stenophyllum**
  5. Fruit in cross-section 4-locular not falsely 10-locular; plants of Costa Rica and Panama ______ **6. V. consanguineum**
 4. Anthers lacking spurs; leaves entire or minutely serrate to crenate-serrulate.
  7. Leaves marginally crenate to very clearly crenate-serrate or minutely glandularly serrulate.
   8. Leaf-blades basally broadly cordate, mostly 2–5 cm broad ______ **7. V. cordifolium**
   8. Leaf-blades basally acute to rounded, mostly less than 2 cm broad.
    9. Leaves glabrous on both surfaces, 8–15 cm long and 4–8 cm broad; leaf venation prominently reticulate ______ **8. V. breedlovei**
    9. Leaves glabrous to densely pilose on both surfaces, (0.4–)1–4.5(–7.5) cm long and usually less than 2 cm broad; leaf venation indistinct to moderately reticulate.
     10. Leaf surfaces densely pilose.
      11. Leaf-blades elliptic to ovate-elliptic, 1–1.5 cm long and 3–8 mm broad; petioles 1–2 mm long; corolla 3.5–5 mm long. ______ **9. V. chihuahuense**
      11. Leaf-blades oblong to lanceolate, 3–4.5(–7.5) cm long and 0.8–2(–3) cm broad; petioles 2.5–8 mm long; corolla 8–10 mm long ______ **10. V. lundellianum**
     10. Leaf surfaces glabrous or very nearly so except possibly in the vicinity of the petiole-blade junction.
      12. Corolla tube densely pubescent externally.
       13. Corolla aestivation imbricate, the tube 5–7.2(–9) × 3 mm, glabrous to pilose externally, glabrous internally; leaves lacking basal glands on lower surface; surface of anthers minutely papillose; forested slopes from 1600–3200(–3700) m in southern Mexico southward into Honduras and El Salvador ______ **11. V. selerianum**
       13. Corolla aestivation valvate, the tube 8–13 × 4–6 mm, densely pilose externally, moderately pilose internally; leaves with 1–2 circular basal glands on lower surface; surface of anthers smooth; forested slopes and páramo from 2500 m and above on Cerro Chirripó, Costa Rica ______ **12. V. talamancense**
      12. Corolla tube externally glabrous or at most with a few scattered trichomes.
       14. Pedicels 7 mm long or less; calyx lobes 1.5 mm long or less.
        15. Leaf-blades mostly over 2 cm long.
         16. Racemes 5–16-flowered, the peduncle/rachis arising from the axils of subtending foliage leaves or from subtending leaf scars, mostly (1.5–)5–9 cm long; corolla broadly campanulate to urceolate or cylindric, 3–6 mm long; berry clearly falsely 10-locular ______ **4. V. leucanthum**
         16. Racemes 6–12-flowered with the peduncle and rachis together mostly 0.3–1.2 cm long; corolla cylindric, 5–9 mm long; berry 4–5-locular ______ **11. V. selerianum**
        15. Leaf-blades mostly less than 2 cm long.
         17. Corolla cylindric, 5–6.5 mm long; Costa Rica ______ **13. V. floribundum**
         17. Corolla cylindric to cylindric-campanulate or cylindric-urceolate, 4–6.5 mm long; Mexico, Guatemala, and Honduras ______ **14. V. confertum**
       14. Pedicels (8–)12–14 mm long; calyx lobes ca. 2 mm long ______ **15. V. wilburii**

7. Leaves entire.
 18. Calyx basally closely subtended or even slightly clasped by 2 broad, rounded bracteoles; pedicels shorter than the flowers; corolla bright red ____ **3. V. dissimile**
 18. Calyx not closely subtended by slightly clasping bracteoles; pedicels much longer than the flowers; corolla not red, but rather often yellowish- or creamy-green.
  19. Secondary and tertiary leaf veins strongly elevated beneath forming a coarse reticulum.
   20. Petioles 5–9 mm long; calyx lobes 5–6 mm long, conspicuously nerved; filaments ca. 3 mm long ____ **16. V. jefense**
   20. Petioles 2–4 mm long; calyx lobes 1–1.2 mm long; filaments 2–2.5 mm long ____ **17. V. furfuraceum**
  19. Secondary and tertiary leaf veins together neither strongly elevated nor forming a pronouncedly elevated reticulum.
   21. Calyx limb saccate, 5(–10)-spurred opposite and below each lobe ____ **18. V. luteynii**
   21. Calyx limb terete and unlobed.
    22. Calyx lobes (1.8–)2–5 mm long.
     23. Leaves conspicuously bullate, the bases ± clasping, the apices rounded; calyx pilosulose ____ **19. V. bocatorense**
     23. Leaves flat not bullate (sometimes concave in *V. monteverdense*), the bases clearly not clasping, the apices acute to acuminate; calyx glabrous.
      24. Corolla internally densely floccose with a dense tangle of white, villous trichomes; anther tubules ca. 1–1.2 mm long ____ **20. V. floccosum**
      24. Corolla internally glabrous; anther tubules ca. 3–5 mm long.
       25. Lower leaf surface glabrous; petioles 4–8 mm long, glabrous or nearly so; pedicels and rachises glabrous; calyx tube 4.5–8.5 mm long; calyx lobes 2.5–3.5 mm long; anthe tubules 4.8–5 mm long, pilose along inner surfaces ____ **21. V. monteverdense**
       25. Lower leaf surface moderately beset with minute puberulence; petioles 3–4 mm long, minutely puberulous; pedicels and rachises puberulous to short pilose; calyx tube 2–3.5 mm long; calyx lobes 4–5 mm long; anther tubules 3–4.6 mm long, glabrous along inner surfaces ____ **22. V. campanense**
    22. Calyx lobes 1.5 mm long or less.
     26. Corollas cylindric to cylindric-campanulate, (5–)8–12 mm long, glabrous internally; staminal filaments noticeably shorter than anthers, the anther tubules 3 mm or longer.
      27. Petioles 1–4 mm long; corollas 8–12 mm long and 6–10 mm in diam. ____ **23. V. poasanum**
      27. Petioles 6–15 mm long; corollas 5–9 mm long and 4–6 mm in diam.
       28. Leaf venation plinerved; calyx lobes 0.2–0.4 mm long or less; corollas pale green to white; anther tubules dehiscing by terminal pores ____ **24. V. almedae**
       28. Leaf venation pinnate; calyx lobes ca. 0.6 mm long or longer; corollas light pink or greenish-white; anther tubules dehiscing by elongate, latrorse clefts ____ **25. V. santafeense**
     26. Corollas cylindric to urceolate, 5–8 mm long, pilose internally; staminal filaments about equaling anthers or slightly shorter, the anther tubules less than 2 mm long.
      29. Leaf-blades basally acutely tapering to rounded; calyx lobes 1.2–1.8(–2) mm long ____ **26. V. costaricense**
      29. Leaf-blades basally rounded to more typically cordate and amplexicaul; calyx lobes 0.8–1.2 mm long ____ **27. V. orosiense**

1. Vaccinium kunthianum Klotzsch, Linnaea 24:56. 1851. Type: based on the accounts of HBK (1818) and Dunal (1838) cited below. *Polycodium kunthianum* (Klotzsch) C.B. Rob., Bull. Torrey Bot. Club 39:559. 1912.

Vaccinium stamineum L. var. *ß* Kunth in H.B.K., Nov. Gen. Sp. Pl. 3:267, t. 253. 1818. Type: MEXICO. Hidalgo: "in sylvis Mexicanis, inter Pachuca et Real del Monte, alt. 1420 hex," *Bonpland s.n.* (holotype: B†; lectotype, designated here: P-H&B). The specimen of var. *ß* (=*V. kunthianum*), which is in the Humboldt and Bonpland herbarium in Paris (P-H&B), is herewith designated as the lectotype; it is without collection number. There is also at P another sheet annotated by Sleumer in 1958 as an isotype of *Vaccinium kunthianum*; it has the collection number of *Bonpland 4079*. The Ericaceae at Berlin (B) were all destroyed during World War II. The Field Museum neg. 9020 of the B type shows a sheet with a hand-written label that gives the locality as "in sylvis Mexicanis prope Real del Monte" and the collection number as "*Bonpland 4074, 4079*." The photo also shows two plant specimens, perhaps the one on the left is "4074" and the one on the right "4079," but there is no way to tell. The type fragment at F has the collection number as "*Bonpland 4079*."

The Ericaceae types of the Willdenow Herbarium (B-Willd.) include a specimen "America meridionalis, leg. *Humboldt & Bonpland s.n.*" (B-Willd. 8312-1), which has a label written by Klotzsch "*Vaccinium Kunthianum* Kl." This is probably an isotype, but does not have a Humboldt & Bonpland collection number associated with it.

Vaccinium elevatum Banks & Solander ex Wikst. var. *ß* Dunal, DC. Prodr. 7:568. 1838. Type: same as for *V. stamineum* var. ß above.

Terrestrial *shrubs* (1–)1.5–10 dm tall; branchlets densely and softly pilosulous or puberulent, the trichomes throughout usually slender and hyaline but occasionally some gland-tipped. *Leaf-blades* deciduous, membranous, elliptic to oblong-elliptic or ovate-oblong, 1.5–3.5(–6.5) cm long, 5–12(–2.2) mm broad, apically acute to rounded, basally acutely tapering to rounded, marginally entire and sometimes strongly revolute, densely spreading pilosulose on both surfaces or glabrate, the venation pinnate but only the midrib conspicuous above, although the lamina also somewhat pustular above, all nerves raised and conspicuous beneath; petioles ca. 1–2.5 mm long, subterete but narrowly canaliculate above, densely puberulent or pilosulose as branchlets. *Inflorescences* axillary, of often leafy racemes, 3–8-flowered; rachises sharply angled, 4–34 mm long, pubescent as branchlets; floral bracts leaf-like to leafy, persistent, elliptic, acute, 5–15 mm long, glabrous to pilosulose abaxially; pedicels 5–6 mm long, sometimes nodding, pubescent as branchlets; bracteoles basal or near base, linear to oblanceolate, ca. 1.5–3 mm long, hirsutulous. *Flowers* 5-merous; calyx ca. 2.5–4.5 mm long, continuous with pedicel although rarely appearing articulate as fruit matures, the tube campanulate and ± flaring distally, ca. 1–1.5 mm high and 2 mm in diam., glabrous to densely hirsutulous with white, downwardly reflexed, delicate, white trichomes, the limb flaring above, glabrous to pilosulose, the lobes deltoid, acute to obtuse, ca. 1–2 mm long, ciliate or puberulous to pilosulose; corolla with aestivation open, membranaceous, unistratose, campanulate, ca. 4.7–6(–8) mm long, white, glabrous, deeply-lobed, the lobes deltoid to oblong, acute to rounded, ca. 3–4 mm long; stamens 10, conspicuously exserted (rarely included), ca. (4.8–)8.5 mm long, the filaments ca. (2.7–)3 mm long, flattened, densely hirsutulous externally and glabrous internally, the anthers ca. (3–)5–6.5 mm long, bearing dorsally, ascending or horizontally widespreading, slender, finely muricate spurs ca. 0.7–2 mm long, the thecae ca. (1.3–)2–2.5 mm long, sharply and finely muricate, the tubules ca. (1.7–)3–4.5 mm long, muricate, dehiscing by short, introrse, slightly oblique pores that are marginally irregularly 2–4-dentate (lacinate); styles long-exserted, to 11 mm long. *Berry* spherical, 5–10 mm in diam., black, sparingly to moderately pilosulose, 5-locular (?).

Distribution.—Montane forests, dry pine forests, and oak-pine forests of the Sierra Madre Oriental of Mexico from Nuevo León and Tamaulipas, south through San Luis Potosi, Puebla, Hidalgo, and Vera Cruz, at 1550–1785 m. Flowering: Apr–Jul; fruiting: Jun–Sep.

Vaccinium kunthianum is characterized by a calyx that is continuous with the pedicel, a corolla that is open prior to anthesis and enlarges thereafter, by anthers conspicuously exserted beyond the corolla tube, and by anther spurs present.

This is the only Mexican representative of the very distinctive subgenus *Polycodium* (Raf.) [= sect. *Polycodium* (Raf.) Rehder], a largely eastern North American taxon often treated as the separate genus *Polycodium* Raf. It is all too easy for us to discount Rafinesquian genera out-of-hand, but this segregate genus does have the independent approbation of Nuttall (1843), one of our historically most critical and acclaimed botanists, who segregated this group of species from *Vaccinium* as the genus *Picrococcus* Nutt. The systematics of *Polycodium* whether treated as a section, subgenus, or genus is unresolved. As many as 20 species or as few as one species (Baker 1970) have been recognized. Recently, Vander Kloet (1988) recognized a single species in eastern North America, *V. staminium* L., while relegating the Mexican outliers in the Sierra Madre Occidentale to synonymy. Too little material is available to be dogmatic, but the Mexican plants seem very unlike the common *V. stamineum* of eastern North America. Therefore, for the present the *Vaccinium kunthianum* is best treated as a distinct species. Like almost all species in Mexico and Central America much more intensive field observation and collecting is needed.

Additional collections examined: **MEXICO. Nuevo León:** oak-pine forest 8 mi E of Dulces Nombres, 1550 m, 30 Jun 1948, *Meyer & Rogers 2708* (MO); abundant in open pine forest and oak scrub, La Trinidad, Municipio de Mantemorelos, 19 Aug 1939, *Muller 2843* (GH, LL, NY). **Taumaulipas:** Sierra de Guatemala, 23°5-7'N, 99°15'W, just W of Tierra Colorado, 19–25 Aug 1984, *Johnston 12813* (TEX). **San Luis Potosi:** Cerro El Agujón, cerca de El Zapote, approx. 30 km al SSW de Río Verde, 1750 m, 13 May 1968, *Rzedowski 25675*

(CAS, LL, MICH, MSC, RSA, WIS). **Puebla:** dry pine forests near Honey Station, 5800 ft, May 1904, *Pringle 8899* (CAS, CU, F, GH, K, MO, MIN, MSC, NY, PH, US). **Hidalgo:** on road to Encarnación from km. 240 on Pan-American Hwy., 2 Jun 1948, *Atchinson 512* (CU); Zimapán, *Coulter 892* (CGE, GH, K, NY, PH); District Zacualtipján pine woods and sphagnum bogs ca. 3 mi from Zacualtipán on road to Tianguistengo, 2100 m, 4 Jul 1947, *Moore 3305* (CU, GH). **Veracruz:** Municipio de Zacualpán, 2500–2600 m, 20°24'W, 98°26'W, 9 mi SE of Palo Bendito, bosque de piños, 22 Jul 1982, *Nee & Diggs 25228* (F).

2. Vaccinium geminiflorum Kunth in H.B.K., Nov. Gen. Sp. Pl. 3:267, t. 252. 1818. Type: "Crescit in Regno Mexicano, inter Omitlan et Moran, alt. 1400 hex," (holotype: P-HBK!; isotypes: B†, B-Willd. 8315-1!). The isotype in the Willdenow Herbarium has on its label "*leg. Humboldt & Bonpland s.n.*" and "*Vaccinium geminiflorum* H.B.K." written by Klotzsch (P. Hiepko 2007 to JLL).

Erect, rhizomatous, densely branched *shrublets* mostly 10–25 cm tall, often forming dense colonies, glabrous throughout with the exception of the youngest stems and leaves; branchlets angled, at first densely but minutely puberulent but becoming glabrate. *Leaf-blades* deciduous or briefly persistent, membranous, oblanceolate or narrowly oblong-obovate to somewhat elliptic, 5–20(–32) mm long, 3–8(–12) mm wide, apically obtuse to acute, basally narrowed to a ± cuneate base, marginally finely crenate-serrulate with the teeth usually terminated especially when young with a very short, gland-tipped vein, both surfaces glabrous but the veins (especially when young) often very minutely and sparsely puberulous, the venation pinnate, forming a conspicuous, elevated reticulum on both surfaces at least when dried; petioles 1–2 mm long, semicircular in cross-section, flatly grooved above, glabrous. *Inflorescences* axillary, of solitary flowers; floral bracts leaf-like in shape and texture, 4.5–6 mm long; pedicels recurved, 3–5 mm long, slightly and very shortly puberulous to glabrous; bracteoles basal, caducous, oblong, rounded, ca. 4–5 mm long, covering pedicel and calyx. *Flowers* 5-merous; calyx 2–3 mm long, continuous with pedicel, the tube campanulate, ca. 1.4–1.8 mm long, glabrous, the limb distally truncate to minutely lobed, the lobes obscure to broadly ovate, apically rounded to apiculate, ca. 0.3–1 mm long, glabrous, occasionally with minute, glandular (glaucous?) scales; corolla with aestivation imbricate, membranous, unistratose, cylindrical to more typically squatly barrel-shaped or globose-urceolate, 4–6 mm long, 3–4 mm broad, white to pinkish or even roseate, glabrous, the lobes broadly rounded, 0.8–1.5 mm long; stamens 10, included, ca. 3.5–4.5 mm long, the filaments ca. (1–)2–2.4 mm long, glabrous, the anthers ca. 2.5 mm long, dorsally bearing 2, slender, antrorsely and minutely barbellate, strongly ascendent spurs ca. 0.6–2.2 mm long, the thecae ca. (0.5–)1–1.4 mm long, papillose, the tubules ca. 0.9–1.7 mm long, 10 or more times as long as wide, dehiscing by oblique or nearly terminal introrse pores. *Berry* dull blackish, unknown at maturity.

Distribution.—Montane pine-oak forests, alpine meadows, boulder fields, and seepage areas, from Chihuahua and Nuevo Leon south throughout much of mountainous Mexico into Guatemala, at 1785–4110 m. Flowering: throughout most of the year but mostly from Feb–Aug; fruiting: Mar–Oct.

Vaccinium geminiflorum is characterized by its subshrub, rhizomatous habit, deciduous (or nearly so) leaves, calyx that is continuous with the pedicel, corolla with imbricate aestivation, long-spurred anthers, and comparatively large and long bracteoles.

The most extensive discussion of the Mexican and Guatemalan members of the *V. cespitosum - geminiflorum* complex was that of Camp (1942), based largely on his observations in western Mexico. Vander Kloet (1988) recognized both *V. cespitosum* Michx. and *V. geminiflorum* Kunth as occurring in Mexico with *V. cespitosum* represented by "one disjunct population" although his map shows three widely separated localities in western Mexico. Camp noted that the plants of *V. geminiflorum* from lower elevations, seldom if ever subjected to frost, had persistent leaves while those from higher elevations had deciduous leaves. Roughly correlated with persistence and lower elevations were more deeply grooved twigs and narrow, relatively longer leaves at the lower elevations, while at higher elevations the twigs are more likely to be subterete and the leaves wider. Camp concluded that because of the morphological intergradation that it would be best to maintain the Mexican material of this complex or section under a single name, *V. geminiflorum*. He speculated that in the Pleistocene the widespread northern *V. cespitosum* had had to migrate into Mexico where it encountered *V. geminiflorum* and hybridized with it resulting in the great variability in the populations encountered in the mountains of central Oaxaca. We are unable to evaluate this suggestion.

The focus of vander Kloet's earlier publications was upon the North American representatives of the

genus, but he also delt with the species of "northern Mexico." Only Mexican species whose range was largely in the United States and Canada were included in his account: *Vaccinium cespitosum* Michx. and *V. kunthianum* Kunth (as *V. stamineum* L.). Little material was available to him for study. From vander Kloet's keys and descriptions the following key has been extracted.

Leaf margins sharply serrate along most its length; blade often sparsely glandular beneath; berry dull black; restricted to Mexico and Guatemala ______ **V. geminiflorum**

Leaf margins usually serrulate from the apex to at least the middle of the blade; blade often somewhat glandular beneath; berry usually blue and glaucous, or rarely dull black; ranging from Labrador to Alaska and south into New England, Wisconsin, Colorado and California with three disjunct localities in Mexico ______ **V. caespitosa**

Additional collections examined: **MEXICO. Chihuahua:** Municipio de Bocoyna: E of Creel, on W facing slope in pine-oak forest, ca. 7100 ft, 8 May 1973, *Bye 3690* (TEX); high mountains above Barranca de Cobre, 6–7000 ft, Jun 1892, *Hartman 527* (GH). **Nuevo León:** alpine meadow, 12,500 ft, summit of Cerro Potosí, 24°53'30"N, 100°10'30 W, 19 Jun 1966, *Gilbert 30* (TEX). **Zacatecas:** Sierra de los Huicholes on road NE from San Juan Peyotán, Nayarit, towards Aserradero Tepetates, 5–25 km N of Nayarit-Zacatecas boundary, 2400–2600 m, 13 Jan 1975, *McVaugh 25770* (MICH). **Durango:** high plateau with *Pinus, Quercus, Artostaphylos* and *Garrya*, 55–60 km SW of Durango City on road to La Flor, 2400 m, 16 Sep 1979, *Breedlove 44097* (CAS); 8–10 km al S de El Salto, hacia Pueblo Nuevo, Municipio de El Salto, 2000 m, 3 Jul 1982, *Hernández & Tenorio 7589* (MO, NY); Laguna del Progreso, 34 road mi N of railroad at Coyotes, lumber camp in dense oak-pine forest on S facing slopes of barranca, 2500–2600 m, 21 Jul 1955, *Maysilles 7887* (MICH). **Hidalgo:** 1.5 km al NNW del Nopalillo, Municipio de Epazoyucan, 2850 m, 14 May 1976, *Medina 1964* (MICH); Peñas Largas, cerca de Tezoantla, Municipio de Real del Monte, bosque de *Abies*, 2750 m, 21 Apr 1966, *Rzedowski 22184* (MSC). **Veracruz:** steep slopes among turf and scattered shrubs and thin pine woods, Mt. Orizaba, 10,400 ft, 28 Apr 1938, *Balls 4384* (A, AAU, K, NY, US); in pine woods, Cofre de Perote, 10300 ft, 2 May 1938, *Balls 4564* (A, K, NY, US). **Puebla:** Ixtaccihuatl, S side of mountain, boulder crevices in alpine meadow, 3960 m, 1 Aug 1958, *Beaman 1995* (GH, MSC); dry pine forests, Honey Station, 5800 ft, Apr 1904, *Pringle 8960* (A, AAU, CAS, CU, F, GH, K, MIN, MO, MSC, NY, PH, US). **Distr. Federal:** in alpine meadow, top of Cerro Ajusco, 3937 m, 12 Jul 1959, *Beaman 2781* (MSC). **Mexico:** grassy ravine in alpine meadow N side of Nevado de Toluca; 0.7 mi E of point where road goes above timberline, 3985 m, 28 Jul 1958, *Beaman 1926* (GH, MSC, TEX, US, WIS); Municipio de Amecameca, slopes of Popocatepetl, ca. 11,000 ft, 4 Jul 1943, *Gily & Dodds 9* (MICH, MSC, NY); Distr. de Temascaltepec, Crucero, grassy hill, 2880 m, 1 Jul 1933, *Hinton 4190* (F, K, MO, NY); rocky moist tussock grassland on very steep slopes, alpine zone on SW slope of Volcán Iztaccihuatl, 5–6 km N of Paso de Cortés, 16 Aug 1960, *Iltis, et al. 1039* (MSC, WIS); Sierra del Monte Alto, Paraje El Guardita, cerca del Cerro La Malinche, 3200 m, 13 Apr 1966, *Rzedowski 22130* (DS, MICH, MSC). **Jalisco:** Nevado de Colima, 12500 ft, 16 May 1893, *Pringle 4375* (F, GH, K, MIN, MO, MSC, MU, NY, PH, US). **Guerrero:** pine forest, Teotepec, Distr. de Miña, 3200 m, 17 Jul 1939, *Hinton et al. 14450* (F, GH, LL, MO, NY, PH, US). **Oaxaca:** top of the mountain just below the stone of sacrifice, Zempoaltepetl, 19–27 Feb 1937, *Camp 2651* (AAU, CAS, DUKE, MICH, MO, NY, US); crest of Mexican Hwy. 175, 30.5 mi N of Guelatao, open, moist, rounded top of mt. ridge, ca. 10,000 ft, 24 Dec 1975, *Reznicek & Gregory 328* (MICH). **Chiapas:** slopes with *Pinus, Quercus* and *Arbutus*, 5 km N of Mexican Hwy. 190 on logging road from Laguna Chamula microwave station, 2400 m, 15 Oct 1976, *Breedlove 40755* (DS). **GUATEMALA. Chimaltenango:** in meadow above timberline, NW side of Volcán Acatenango, ca. 3760 m, 16 Aug 1959, *Beaman 3270* (GH, MSC). **Huehuetenango:** Sierra de los Cuchumatanes, summit between Tojquia and Caxin bluff, 3700 m, 6 Aug 1942, *Steyermark 50214* (A, F, NY, US). **Quezaltenango:** summit of Volcán Santa María, 12,400 ft, 26 Jul 1934, Skutch 837 (A). **Sacatepequez:** summit of S rim of crater, 3760 m, 31 Jul 1959, *Beaman 2925* (GH, MSC, TEX, US). **San Marcos:** in gravelly soil above timberline, E side of peak, Volcán Tajumulco, ca. 4110 m, 9 Aug 1959, *Beaman 3159* (GH, MSC, TEX, US).

3. Vaccinium dissimile S.F. Blake, J. Bot. 53:271. 1915. *Disterigma dissimile* (S.F. Blake) S.F. Blake, Proc. Biol. Soc. Washington 35:120. 1922. *Sphyrospermum dissimile* (S.F. Blake) Luteyn, Opera Bot. 92:126. 1987. TYPE: COSTA RICA. SAN JOSÉ: La Palma, 1500 m, Aug 1898, *Tonduz 12546* distributed as *J. Donnell Smith 7380* (LECTOTYPE: K! ISOLECTOTYPES: BM! F! GH! K! MO! NY! US!).

Creeping, epiphytic or terrestrial, viney *shrublets* with stems interwoven amongst bryophytes; branchlets wiry, perhaps to 1 m long, 1–1.5 mm in diam., the young stems densely spreading puberulent, glabrous in age. *Leaf-blades* persistent, coriaceous, evergreen, ovate, lance-ovate, or narrowly to broadly elliptic, mostly 1–3(–4) cm long, 8–15(–20) mm broad, apically acute, basally rounded to cuneate, marginally entire, glabrous or beneath sparingly to moderately beset with dark, glandular, appressed trichomes 0.1–0.2 mm long, the venation obscure; petioles 1–2 mm long, puberulent. *Inflorescences* axillary, of solitary flowers; floral bracts broadly reniform, ca. 0.3–0.4 mm long, rounded, glabrous; pedicels 1–2(–4 or –8?) mm long; bracteoles basal, ovate to broadly oblong, opposite, obtuse to broadly rounded, 0.8–1 mm long and nearly as wide, puberulent. *Flowers* 4-merous; calyx ca. 2.2–2.8 mm long, continuous with pedicel, the tube campanulate, 0.8–1.2 mm long, densely hirsutulous with hyaline trichomes 0.1–0.2 mm long, the lobes broadly deltoid, acute, 0.7–0.8 mm long, moderately to densely hirsutulous; corolla with aestivation valvate, thinly fleshy, bistratose, campanulate to broadly flaringly funnelform, 7–10 mm long, 6–9 mm in diam. at the apex or the

broadest point, red, sparingly and inconspicuously beset with spreading, gland-tipped trichomes 0.1–0.2 mm long, the lobes erect, acutely deltoid, 1.5–2 mm long; stamens 8, included, ca. 4.3–5.8 mm long, the filaments 1.3–4 mm long, elliptical, tapering both to the base and the apex where ca. 0.5 mm wide, sparsely pilose, the anthers medifixed, 2–3.3 mm long, lacking spurs, the thecae ca. 1.7 mm long, conspicuously papillose, the tubules 1.6–2.5 mm long, dehiscing by introrse clefts 0.5–0.7 mm long. *Berry* bluntly 4-angled, oblate, 0.7–1 cm in diam., translucent white, densely hirsutulous, 4-locular.

Distribution.—Wet mountain slopes dominated by premontane rainforests and elfin thickets of shrubs and small trees in Costa Rica and Panama and also in NW South America (Colombia and Ecuador), at 500–1800 m. Flowering and fruiting: throughout much of the year but perhaps heaviest from Feb–Aug.

Vaccinium dissimile is characterized by its lianoid, thin-stemmed habit, short pedicels, and dark red, campanulate corollas. This is another species of *Vaccinium* that rests not too comfortably with its supposed congeners. S.F. Blake, who orginally named the species as a *Vaccinium*, later transfered it into the genus *Disterigma*. Luteyn, currently the leading authority on the neotropical representatives of the family, has concluded that this species should be placed in the genus *Sphyrospermum* Poeppig & Endlicher as shown by the mature fruit: "The fruits of *Vaccinium* and *Disterigma* (and most ericaceous blueberries) have a thick and leathery pericarp that dries that way, and the seeds have normal embryos whereas in *Sphyrospermum* and *Themistoclesia* the pericarp is very thin and papery ... and the seeds have a green embryo ..." (Luteyn 1987, p. 126). [Note: RLW, first author of this paper, wishes to treat this species in *Vaccinium*; JLL, second author of this paper, however, disagrees and still maintains the species belongs in *Sphyrospermum*.]

Additional collections examined: **COSTA RICA. Heredia:** forest along new road to the N of Quebrada Tigre from Finca El Plastico to ca. 1.5 km NE thereof, ca. 8 km SW of Las Horquetas, 10°18'N, 84°02'W, 450–550 m, 14 Feb 1986, *Grayum & Sleeper 6510* (DUKE, MO). **San José:** forested thickets and weedy roadside at Alto La Palma ca. 8 mi NNE of San Vincente de Moravia on the eastern flank of Volcán Barba, ca. 1500 m, 23 May 1972, *Wilbur & Almeda 16898* (CAS, CR, DUKE, F, GH, LL, MICH, MO, NY, US, PMA, WIS). **PANAMA. Bocas del Toro:** Cerro Colorado, road along top, 1500–1750 m, 13 Aug 1977, *Folsom et al. 4726* (DUKE); forested slopes, Fortuna Dam region, along trails leaving pipeline road, ca. 8°45'N, 82°15'W, ca. 1000 m, 8 Dec 1985, *McPherson 786* (DUKE, MO). **Chiriquí:** cloud forest, Cerro Colorado, ca. 50 km N of San Félix, ca. 1400 m, 17 Aug 1975, *Dressler 5086* (DUKE, MO). **Veraguas:** 11 km from Escuela Agrícola Alto de Piedra, in forest along Río Dos Bocas, Atlantic slope, 15 Nov 1974, *Mori & Kallunki 3147* (MO). **Coclé:** Cerro Pajita, hills N of El Valle, 1100 m, 27 Oct 1946, *Allen 3782* (MO, US); Atlantic slope near sawmill above El Cope, 8°40'N, 80°36'W, 750–800 m, 13 Feb 1982, *Knapp & Dressler 3494B* (DUKE, MO); La Mesa, 5 mi N of El Vallé, 2500 ft, 10 Nov 1965, *Tyson & Godfrey 2443* (DUKE, MO). **Panamá:** Cerro Jefé, new road leading N from summit, 26 Sep 1975, *Witherspoon 8526* (DUKE, MO). **Colón:** S approach of Cerro Bruja from Río Escandaloso, 18 May 1978, *Hammel 3123* (MO). **San Blas:** premontane rain forest, Cerro Brewster, 9°18'N, 79°16'W, 800–850 m, 20 Nov 1985, *de Nevers et al. 6269* (DUKE, MO). **Darién:** Sambú Basin, Cerro de Garagara, 500–974 m, 7 Feb 1912, *Pittier 5644* (US).

4. Vaccinium leucanthum Schltdl., Linnaea 8:524. 1833. Type: MEXICO. VERACRUZ: "infra S. Salvdor...Pr. Chiconquiaco" [in mountains up to 6000 ft between Misantla and Jalapa], *Schiede 174* (holotype: B†; lectotype, designated here: NY! isolectotypes: K! MO! P! W!). [The label of the NY sheet (ex Meisner herb.) reads "Infra S. Salvador, Mexico"; the K sheet reads "pr. Chiconquiaco" and is without a collection number; the MO sheet reads simply "Mexico."]

Vaccinium schlechtendalii G. Don, Gen Syst. 3:856. Nov 1834. Type: MEXICO: "near Jalacinga, in woods." The actual collection and location of Don's type specimen is unknown. *Metagonia schlechtendalii* (G. Don) Nutt., Trans. Amer. Phil. Soc. n.s. 8:266. 1843.

Vaccinium micranthum Dunal, Prodr. 7:568. 1839. Type: MEXICO: "inter Tampico et Real del Monte," *Berlandier 329 (pl. exs. n. 12)* [HOLOTYPE: G-DC (photos F neg. 33846 and NY neg. s.n.); isotypes: BM!, NY frag. ex G-DC!, OXF! P!]. The type specimen in the DeCandolle Herbarium (G), as seen in person (JLL) has a label that gives the number "*12 ex.*" in the upper left corner and the number "*329*" in the upper right corner. There is a fragment of the G-DC type at NY, three specimens of *Berlandier 329* at P!, and one each at the BM and OXF (all isotypes). The actual collection number is *Berlandier 329* and the collection is number 12 in an exsiccatae sent out by Berlandier. It is also possible that the plants named by George Don (1834) and by Dunal (1839) are the same collection.

Terrestrial *shrubs* 1–4.5 m to *trees* to 15 m tall; branchlets somewhat angulate when young but becoming terete, minutely but densely puberulent or glabrate. *Leaf-blades* persistent, coriaceous, evergreen, lanceolate to lance-oblong to ovate, highly variable in shape and size, mostly 2–5(–7.5) cm long, 1.2–2.6 cm broad, apically usually acute to less commonly obtuse or rounded, not mucronate, basally cuneate to rounded, marginally crenate-serrate, when mature glabrous or at most very sparingly puberulous (or even densely but often inconspicuously so along the midrib above), when young glabrous to densely puberulous beneath with midrib puberulous above, rarely glandular-punctate beneath, the venation pinnate; petioles 2–4 mm long,

semicircular in cross-section, broadly and shallowly grooved above, glabrous to densely short-puberulous. *Inflorescences* axillary, sometimes arising from leafless nodes, racemose, 5–16-flowered; rachises finely ridged and grooved, (1.5–)5–9 cm long, 0.5–1 mm in diam., densely to sparsely but minutely puberulent; floral bracts caducous, oblong, cuculate, ca. 1.5–4 mm long, 2–2.5 mm broad; pedicels nodding, often somewhat secund, ca. 1.5–7(–12) mm long, finely but densely to sparsely puberulent; bracteoles located medially to just above or below middle, ± opposite, caducous, linear, 1.5–2.5 mm long, glabrous to puberulous, caducous. *Flowers* (4–)5-merous; calyx 2.5–2.7 mm long, conspicuously articulate with pedicel, the tube obconical, 1–1.5 mm long, sparingly to very densely puberulent, the lobes deltoid, acute, 0.8–1.5 mm long; corolla with aestivation imbricate, membranous, unistratose, broadly campanulate to urceolate, 3–6 mm long, white to pinkish tinged, glabrous externally, the lobes deltoid, acute, 1–2.2 mm long; stamens (8–)10, included, 2.8–5.4 mm long, the filaments ca. 1–3.2 mm long, ciliate distally, the anthers 1.7–3.4 mm long, typically bearing dorsally 2, slender, strongly ascendent and outwardly divergent spurs ca. 0.6–1.2 mm long but these apparently sometimes represented by vestigial remnants 0.1–0.5 mm long, the thecae ca. 1–1.5 mm long, the tubules ca. 0.7–2 mm long, dehiscing by short, oblique, introrse, oval pores; nectariferous disk glabrous. *Berry* spherical, ca. 5–8 mm in diam., blackish, puberulous to glabrate, falsely 10-locular.

Distribution.—Montane pine-oak and both evergreen and deciduous forests, thickets and clearings from Hidalgo south through Vera Cruz into Michoacán, Oaxaca, and Chiapas (Mexico), and much of mountainous Guatemala to Honduras, mostly between 1500–3000 m. Flowering: throughout the year but peaking from Apr–Jul; fruiting: throughout the year.

Vaccinium leucanthum is characterized by its broad, crenate-serrate leaves, long-racemose inflorescences, its calyx articulate with the pedicel, spurred to unspurred anthers, and a falsely 10-locular berry. No other species of *Vaccinium* in either Mexico or Central America has proven as baffling as *V. leucanthum*. As interpreted in this treatment, it has the greatest range of floral morphological variability of any species in the area. On numerous occasions it was felt that a set of characters had been detected that would allow the clean separation of a block of disconcerting variability but analysis of more specimens dashed the supposed solution. The most strikingly variable features are in leaf size and shape, number of perianth parts, and length of the anther spurs. The variablility of spur length proved especially vexing for *a priori* it was felt that spur length was of "fundamental" importance. These spurs ranged from slender, upwardly arching, long, horn-like appendages to the merest protuberance and in some cases could not be detected with certainty and so might well be absent. The presence or absence of spurs has usually been treated as of sectional, subgeneric or even generic significance within the Vaccinieae. Belatedly and no doubt reluctantly, it was impossible to employ anther spurs as a taxonomically useful character in this species. This is not a wholly satisfactory solution; it just happens to be the best that can be done now. Extensive field work throughout the range of *V. leucanthum* would probably be most helpful in resolving the apparent uncertainties. It would also appear that the problems associated with this species can only be resolved in conjunction with its relatives in the Andes of South America and the West Indies.

Additional collections examined: **MEXICO. Hidalgo:** Dist. Tulancingo, dry ravine and ridges in pine-oak woods near Rancho San Alajo between Tulancingo and Acaxochitlán, 7000 ft, 13 May 1947, *Moore 2820* (CU, GH, MICH); hills ca. Trinidad Iron Works, 5800 ft, 6 May 1904, *Pringle 8883* (A, CAS, CU, F, GH, LL, MIN, MO, MSC, PH, US). **Veracruz:** Perote, La Joya, 6500 ft, on old lava in crevices and partial shade of open woods of *Pinus*, 23 Sep 1938, *Balls 5519* (GH, US); Ocotepec, cerca del Cerro, Municipio de Jalacingo, 1800 m, bosque de encino, ladera de cerro, 4 Mar 1970, *Ventura A. 1006* (DS, F, MICH, MO, NY). **Puebla:** mountain forest W of Huauchinango, 1 Nov 1943, *Lundell 12640* (GH, MICH, MO, NY, US); in *Pinus-Quercus-Podocarpus* forest, near hwy. between Beristáin and Huauchinango, *Ogden & Gilly 51212* (DUKE, MICH). **Michoacán:** bosque de pino, San Miquel del Monte, 15 km al SE de Morelia, 2200 m, 17 Sep 1967, *Rzedowski 25165* (CAS, LL, MICH, MSC). **Oaxaca:** very wet forest of pines, oaks and other trees, along road from Teotitlán del Camino to Huautla de Jiménez, 2250–2300 m, 12 Jul 1968, *Anderson 4739* (DUKE, MICH, NY); top of Zempoaltepetl, 19–27 Feb 1937, *Camp 2660* (AAU, CAS, DUKE, F, GH, MO, US); Villa-Alta, Yalina, El Rincon, 4–6500 ft, *Galeotti 1809* [NY; not a type of *V. caracasanum* Kunth (1818), the name was only misapplied by Martens and Galeotti (1842)]. **Chiapas:** slope with *Quercus* on boundary between Zinacantán and Chamula along road to Zinacantán Center, 7800 ft, 20 Jan 1965, *Breedlove & Raven 8135* (DS, F, LL, MICH, MSC, WIS); steep wooded slopes on the bank of the Río Hondo 4 mi N of Jitotol on road to Pueblo Nuevo Solistahuacán, Municipio de Jitotal, 5500 ft, 31 May 1965, *Breedlove 10178* (DS, F, LL, MICH); evergreen cloud forest on the N and W slope of the Cerro Mozotal below the microwave tower along

the road from Huixtla to El Porvenir and Siltepec, Municipio de Motozintla, 3000 m, 28 Jun 1972, *Breedlove 25827* (DS, DUKE, MICH, MO, NY, RSA); steep slopes with montane rain forest-evergreen cloud forest and elfin forest on the SE side of Cerro Tres Picos and the ridges near summit, 2100–2500 m, 11 Dec 1972, *Breedlove & Thorne 30138* (DS, DUKE, F, MICH, MO, NY, RSA, TEX); Sierra Madre de Chiapas, *Pinus-Liquidambar* forest, between Finca Liquidambar and Neuva Colombia, 2500 m, 18 Jun 1985, *Luteyn & Lebrón-Luteyn 11574* (MEXU, MO, NY). **GUATEMALA. Bajo Verapaz:** open areas above Santa Catarina, 5000 ft, 24 Feb 1945, *Sharp 45254* (GH). **Chiquimula:** mixed forest below cloud forest, middle slopes of Montaña Norte to El Jutal on Cerro Brujo, SE of Concepción de las Miñas, 1700–2000 m, 2 Nov 1939, *Steyermark 31056* (F). **Huehuetenango:** dry roadside bank, 8100 ft, road #9 ca. 13.3 mi S of Santa Eulalia, Sierra de los Cuchumantanes, 31 Dec 1972, *Almeda & Luteyn 1689* (DUKE, F, MICH); bushy mountain side, Soloma, 7400 ft, 21 Aug 1934, *Skutch 1059* (A, F, NY, US). **Progreso:** on summit of Volcán Siglo, 3300 m, 21 Jan 1942, *Steyermark 43080* (A, F). **El Quiché:** in arroyo, Nebaj, 5 Jun 1964, *Contreras 4883* (CAS, GH, LL); trail between Nebaj and Chajul, 6 Feb 1946, *Sharp 4666* (GH, MO, NY). **Zacapa:** trail between Santa Rosalia de Marmol and Vegas, 19 Jan 1942, *Steyermark 42912* (F). **HONDURAS. Comayagua:** "Camp Don Thomas," 10 km SW of Gracias, 1850–2050 m, 10 May 1992, *D'Arcy 17889* (MO); **Cortes:** Cusuco National Park, trail from Cerro Cantiles to Cerro Jilinco, 2240 m, 20 Mar 1993, *Hawkins 659* (MO); **Lempira:** montaña de Celaque, 2650 m, 18–22 Nov 1974 (MO); Parque Nacional Celaque, cloud forest on ridge to Cerro Oeste del Río Naranjo, 2300 m, 9 Jul 1991, *House 1036* (MO).

5. Vaccinium stenophyllum Steud., Nomencl. Bot. 2:740. 1841.

Vaccinium angustifolium Benth., Pl. Hartweg, 45. 1840, non Aiton (1789). TYPE: MEXICO. JALISCO: "in regione frigida prope Bolaños," *Hartweg 342* (HOLOTYPE: K-Herb. Benth.! photos Univ. Michigan neg. 694 and NY neg. s.n., frag. NY; ISOTYPES: BM! CGE! K-Herb. Hook.! NY! OXF! P!).

Vaccinium angustifolium Benth. var. ß *glaucescens* Benth., Pl. Hartweg, 45. 1840. *Vaccinium glaucescens* (Benth.) Riley, Kew Bull.185. 1922. TYPE: MEXICO. JALISCO: "in regione frigida, prope Bolaños," *Hartweg 342B* (HOLOTYPE: K-Herb. Benth.! photo NY neg. s.n., frag. NY!).

Vaccinium gonzalezii Riley, Kew Bull. 116. 1923. TYPE: MEXICO. SÍNALOA: San Ignacio, Mesa de Bueso, 1250 m, *Gonzalez 839* (HOLOTYPE: K! frag. NY!; ISOTYPE: K!).

Terrestrial *shrubs* or small *trees* 1–4(–6) m tall; branchlets slender, glabrous to densely, shortly puberulous, sometimes glaucous. *Leaf-blades* persistent, coriaceous, evergreen, narrowly lanceolate, lance-elliptic to linear-oblong, 1–4(–6.5) cm long, (4–)8–12(–15) mm broad, apically acute to acuminate, shortly and deciduously mucronate, basally cuneate, marginally entire to minutely serrulate with the teeth often glandular-tipped, lustrous above, glabrous or very nearly so on both surfaces except often densely puberulous along the midrib above, the venation pinnate, conspicuously reticulate and often raised on both surfaces; petioles 1–2(–3) mm long, subterete to broadly and shallowly canaliculate above, glabrous to densely although minutely puberulent. *Inflorescences* axillary, either leafy racemes of 3–10 flowers each, **or** flowers solitary in axils of apparently normal or reduced leaves at tips of branchlets and then inflorescences apparently differing little from leafy, vegetative branchlets; rachises (when present) finely ridged and grooved, mostly (1.5–)3–6 cm long, ca. 1 mm in diam., puberulent to glabrous, sometimes glaucous; floral bracts slightly smaller than the foliage leaves and of similar shape and texture, 8–30 mm long, 2.5–9 mm broad, puberulent to glabrate; pedicels nodding or at least strongly divergent, mostly (2–)4–8(–10) mm long, 0.2–0.3 mm in diam., glabrous or sometimes puberulent, sometimes glaucous; bracteoles nearly basal, caducous, subopposite to clearly alternate, oblong to lance-elliptic or linear, 1.2–2.2 mm long. *Flowers* 5-merous; calyx 3.5–4.6 mm long, conspicuously articulate with pedicel, puberulent to glabrous, sometimes glaucous, the tube obconic to somewhat campanulate, 1.5–2 mm long, the lobes deltoid, acute to acuminate, ca. 1.2–2 mm long, glabrous to densely ciliolate at tips; corolla with aestivation imbricate, membranous, unistratose, cylindric to urceolate, 5–7 mm long, whitish to creamy, glabrous externally, the lobes deltoid, acute, 1.2–2.2 mm long; stamens 10, included, 3.5–4.3 mm long, the filaments ca. 1–1.6 mm long, weakly to densely ciliate, the anthers ca. 2.8–3.5 mm long, dorsally bearing slender, strongly ascendent spurs 0.6–1.4 mm long, the thecae ca. 1–1.7 mm long, the tubules slender, 1.2–1.8 mm long, dehiscing by short, introrse, oblique pores; styles included; nectariferous disk glabrous to shortly and densely white-pilose. *Berry* spherical, 5–9 mm in diam., blackish, puberulous or glabrous, sometimes glaucous, falsely 10-locular.

Distribution.—Mountain slopes of the Mexican Sierra Occidentale from Durango south into Oaxaca (Durango, Sínaloa, Nayarit, Jalisco, and Oaxaca), dominated by open pine-oak forests and rocky slopes and summits, mostly between 1075–2800 m. Flowering: (Jan–)Mar–Aug(–Oct); fruiting: (Jan–)Jun–Oct(–Dec).

Vaccinium stenophyllum is characterized by narrowly lanceolate, lance-elliptic to linear-oblong leaves with prominent venation and mucronate tips, inflorescences of leafy racemes **or** flowers solitary in the axils of apparently normal or reduced leaves, a calyx that is articulate with the pedicel, spurred anthers, an often shortly and densely pilose nectariferous disk, and falsely 10-locular berry. Louis Williams (1965, and in Standley & Williams 1966) included *V. stenophyllum* in the *Flora of Guatemala* even though he stated that "the material from Guatemala is hardly, if at all, distinguished from *V. leucanthum*." For this study, no specimens of *V. stenophyllum* have been seen south of Jalisco, while *V. leucanthum* is well-represented in Guatemala. Plants of *V. stenophyllum* are not at all reminiscent of *V. leucanthum*. We agree with Sleumer (1936) that *V. gonzalezii* is merely a broader leaf form of *V. stenophyllum*.

Additional collections examined. **MEXICO. Durango:** bosque 19 km de Los Charcos, por el camino a Sta. María Ocotán, Municipio de Mezquital, 2400 m, 4 Oct 1983, *Gonzalez 2582* (NY). **Sinaloa:** Mesa de Bueso, San Ignacio, 1250 m, 15 May 1919, *Montes & Salàzar 839* (US). **Nayarit:** steep slopes with *Pinus* and *Quercus* along unused road from Mesa del Nayar to Santa Teresa, Municipio de Nayar, 1850 m, 12 Aug 1980, *Breedlove & Almeda 45509* (CAS, MO, NY). **Jalisco:** slope with *Pinus, Quercus* and Arbutus 15 km NW of Los Volcanes on road to Talpa de Allende, Municipio de Aytenguillo, 1890 m, 27 Nov 1983, *Breedlove & Almeda 60617* (CAS, MO, NY); Sierra de Manantlán, 25–30 km SE of Autlán, along lumber roads E of the road crossing called "La Cumbre," between El Chante and Cuzalapa, 19°35'N, 104°8-15'W, summits of high S-facing cliffs, 2750 m, 20–21 Mar 1965, *McVaugh 23131* (MICH); bare, gullied hillside, Hacienda del Cura, Sierra Madre, San Sebastián, 1425 m, 2 Jan 1927, *Mexia 1340* (A, CAS, DS, F, GH, MICH, MO, NY, US); Municipio de San Martín de Bolaños, Las Vidrieras, 10 km al NW de El Platanar, 2450 m, 1 Oct 1968, *Rzedowski 26156* (MICH).

6. Vaccinium consanguineum Klotzsch, Linnaea 24:64. 1861. TYPE: PANAMA: Volcán Chiriquí, *Warszewicz s.n.* (HOLOTYPE: B†, photo F neg. 4613).

Vaccinium irazuense Sleumer, Notizbl. Bot. Gart. Berlin-Dahlem 12:138. 1934. *Vaccinium consanguineum* Klotzsch var. *irazuense* (Sleumer) Sleumer, Notizbl. Bot. Gart. Berlin-Dahlem 13:126. 1936. TYPE: COSTA RICA. CARTAGO: Lava fielder Irazú, *Hoffman 140* (HOLOTYPE: B†, frag. US!).

Terrestrial *shrubs* or small *trees* (0.2–)1–3(–10) m tall, often compact and densely bushy; branchlets stiff, rigid, glabrous to densely puberulent. *Leaf-blades* persistent, coriaceous, evergreen, mostly narrowly to broadly elliptic, occasionally oblong, (1–)1.5–3(–4.6) cm long, 5–12(–18) mm broad, usually 2–3 times as long as wide, usually tapering to an acute apex and base, marginally callose-thickened and shallowly serrulate with teeth mostly (1–)2–4 mm apart, each tooth often tipped with a darkish glandular callosity, glabrous or with scattered glandular fimbriae beneath, moderately puberulous along the midrib, the venation pinnate; petioles 1.5–3 mm long, glabrous or puberulent. *Inflorescences* axillary, racemose, 5–10-flowered; rachises sharply angled, mostly 1–4 cm long, puberulent; floral bracts scarious, ovate to oblong, 2–5 mm long, slightly puberulent or ciliate; pedicels 1–2 mm long, puberulent; bracteoles subopposite, ovate to oblong, scarious, 1.5–3 mm long, ciliate but otherwise glabrous, entire to sparingly and also irregularly and minutely toothed. *Flowers* 4-merous; calyx 3–4 mm long, sharply articulate with pedicel, the tube campanulate, 1–2.3 mm long, glabrous, the lobes deltoid to broadly ovate, 0.8–1.5 mm long, apically ciliate but otherwise glabrous; corolla with aestivation imbricate, membranous, unistratose, cylindric, 5–7.5 mm long, 2.7–4.5 mm in diam., creamy white with tinges of red or pink, glabrous, the lobes oblong, 1–1.7 mm long; stamens 8, included, 4.4–5.7 mm long, the filaments 3–4 mm long, ciliate, the anthers 2.8–4 mm long, bearing dorsally 2, slender, horn-like, ascendent spurs 0.2–0.6(–1) mm long originating from near the apex of the thecae, the thecae 1.5–1.8 mm long, granular-papillate, the tubules 1.2–2 mm long, dehiscing by introrse clefts 0.5–0.7 mm long. *Berry* spherical, 5–6 mm in diam., reddish-to blackish-purple, 4-locular.

Distribution.—Mountain meadows, wooded montane slopes, oak forests, and paramillo thickets in Costa Rica and western Panama (Bocas del Toro and Chiriquí provinces), between (1300–)1500–3500(–3900) m. This species was included by Standley (1920–26, pp. 1101–1102) as a member of the woody flora of Mexico, but its presence north of Costa Rica was questioned by Sleumer (1936) and the species was not included by Standley and Williams in the *Flora of Guatemala* (1966). The species is known only from the mountains of Costa Rica and western Panama. Flowering: throughout the year with the preponderance between Jan–Jul; fruiting: throughout the year.

Vaccinium consanguineum is characterized by its pinnately nerved and serrulate-margined leaf blades,

racemose inflorescences with small white to pink flowers, spurred connectives (these rarely vestigial), and glaucous berries. The species varies from small, densely branched shrubs to large trees to 10 m tall. Leaf size also varies greatly with trees often having leaves at the higher end of the range. The small-leaved populations of *V. consanguineum* look especially like *V. floribundum*. Both species have spurred (or vestigially-spurred) anthers, although the Costa Rican populations of *V. floribundum* lack spurs. Nevertheless, *V. floribundum* would appear to be its closest relative.

Additional collections examined: **Costa Rica. Alajuela:** wooded slopes of Volcán Poás from rim of crater to a distance 2 mi down road towards Varablanca, ca. 8200 ft, 28 Jan 1971, *Wilbur & Teeri 13647* (DAV, DS, DUKE, F, GH, LL, MICH, MO, NY, PMA, TEX). **Heredia:** woods around the Laguna del Barba at 2800 m and on slopes down to ca. 2500 m, 18 Dec 1974, *Wilbur & Luteyn 18375* (DUKE). **Cartago:** upper crest of Volcán Irazú covered with many feet of volcanic ash and bare except for scattered shrubs, 6 May 1971, *Wilbur 14199* (DUKE, F, MO); trail to top of Volcán Turrialba from Finca Quemado between 2800–3200 m, 10 May 1971, *Wilbur 14328* (DUKE); oak dominated slopes ca. 14 km SE of El Empalme, 2600 m, 18 July 1977, *Wilbur et al. 22873* (DUKE, NY). **San José:** roadside slopes ca. 3.4 km SE of La Georgina and 10 km SE of El Asunción, ca. 2750 m, 1 Aug 1977, *Wilbur et al. 23689* (DUKE, NY). **Puntarenas:** Cordillera de Talamanca, 1–3 airline km S of the peak of Cerro Echandi, 9°00'30"-9°01'30"N, 82°49'W, 2500–2800 m, 9 Mar 1984, *Davidse et al. 25492* (DUKE, MO, NY). **Limón:** Cordillera de Talamanca, oak forest at headwaters of the unnamed western branch of the Río Teribe, between Río Sini and the continental divide at Cerro Bekom, 9°10'45"N, 83°03'30"W, 2500–2600 m, 21 & 27 Mar 1984, *Davidse et al. 26142* (CAS, DUKE, MO). **PANAMA. Bocas del Toro:** Cordillera de Talamanca, páramo at main peak of the Cerro Fabrega Massif, 9°07'N, 82°52'40"W, 3100–3300 m, 6 and 8 Mar 1984, *Davidse et al. 25305* (DUKE, MO). **Chiriquí:** forested ridges S of Finca Lerida, 6000–7000 ft, 26 Jul 1947, *Allen 4768* (F, GH, MO, NY, US); western slope of Volcán Chiriquí on open slopes, ca. 9800 ft, *Wilbur et al. 11027* (DS, DUKE, GH, MICH, MO).

7. Vaccinium cordifolium (M. Martens & Galeotti) Hemsley, Biol. Centr. Amer. Bot. 2:274. 1881, where mistakenly printed as *cordatum* – see explanation following description below.

Gaylussacia cordifolia M.Martens & Galeotti, Bull. Acad. Brux. 9:530. 1842, *non Vaccinium cordifolium* Stapf (1894). Type: MEXICO. Veracruz: "croît sur les laves du Pedregal de las Vigas, près de Xalapa, entre 6 et 7,000 pieds d'élévation," *Galeotti 1795* [holotype: BR! (photo NY; barcode BR-S.P 825 928); probable isotypes: BR! (barcode BR-S.P. 825 936), G! (photo F neg. 26634), K! (photo NY neg. 10619)]. The sheet annotated as Holotype by Sleumer in 1965, at BR, has no field locality data on the hand-written label other than "Gay-lussacia cordifolia Nobis. Coll. Galeotti No. 1795." Other handwriting of the labels on the specimens of *Galeotti 1795* at BR, G, and K appears to be similar, based on availble photographs at NY, but the language and exact wording may differ somewhat (i.e., BR Isotype = "Pedregal de las Vigas 6–7000"; G = "sur les laves près Xalapa a 7000"; K = "on the lavas near J[sic]alapa at 7000 ft.").

Vaccinium matudae Lundell, Phytologia 2:4. 1941 [as *matudai*; orthography corrected as advised in ICBN Recommendation 60 C.1.a]. Type: MEXICO. Chiapas: Barranca Honda, Siltepec, growing on rocks, 2600 m, Oct–Nov 1940, *Matuda 4074* (holotype: MICH!; isotypes: A! photo NY neg. 9630, CAS! NY!).

Epiphytic or terrestrial *shrubs*, sometimes arising from lignotubers; branchlets stout, rather irregularly angulate, slightly hirtellous but soon glabrate, reddish. *Leaf-blades* persistent, stiffly coriaceous, evergreen, broadly ovate or oblong-ovate, 2.5–5(–8) cm long, (1.3–)2–3.5(–5) cm broad, apically rounded to subacute, basally shallowly cordate to rounded, marginally subentire to prominently crenate-serrate, glabrous, lustrous, the venation pinnate, slightly elevated above and somewhat more prominently elevated and reticulate beneath; petioles 2–4.5 mm long, ca. 1.5 mm in diam., glabrous or at most very sparingly pilosulose. *Inflorescences* racemose or paniculate, 6–40-flowered, when paniculate then short-pedunculate and to ca. 8 cm long; rachises 3–6 cm long, 1–1.5 mm in diam., glabrous to weakly short-pilose or hirtelous; floral bracts caducous, lanceolate, ciliate, ca. 1.7–3.2 mm long; pedicels erect to secundly nodding, 5–10 mm long; bracteoles nearly basal, lanceolate, ca. 1–2.2 mm long. *Flowers* 5-merous; calyx 4.8–5.3 mm long, conspicuously articulate with pedicel, the tube obconic to campanulate, 2–3.5 mm long, deep rose, glabrous, the lobes deltoid, acute, 1–1.8 mm long, glabrous, non-ciliate; corolla with aestivation imbricate, membranous, unistratose, cylindric to urceolate, 5–8 mm long, whitish tinged with deep pink or rose, glabrous externally, the lobes deltoid, subacute to rounded or obtuse, ca. 1–1.3 mm long; stamens 10, included, 6.5–7 mm long, the filaments ca. 3–4.7 mm long, proximally ciliate, the anthers 3.5–4.2 mm long, lacking spurs, the thecae ca. 1.5–2.2 mm long, pappilose, the tubules ca. 1–2.5 mm long, dehiscing by short, introrse clefts. *Berry* ca. 5–6 mm in diam., 5-locular.

Distribution.—Pine-oak forests, cloud forests, and montain thickets and forests, from the Mexican states

of Vera Cruz through Oaxaca and Chiapas, and mountainous northern Guatemala (Huehuetenango and Quiché departments), between 2000–3100 m. Flowering and fruiting: throughout the year.

Vaccinium cordifolium is characterized by its stiffly coriaceous, broadly cordate leaves with margins subentire to crenate, its racemose (or rarely paniculate) inflorescence, a calyx that is articulate with the pedicel, stamens that lack spurs, and a dark rose to pink corolla.

Vaccinium matudae Lundell, a most distinctive species was first described as *Gay-Lussacia cordifolia* Martens & Galeotti (21842), but was later determined to be a *Vaccinium* by Hemsley (1881). In attempting to form the new combination based on Martens and Galleotti's binomial, he instead unfortunately published *Vaccinium cordatum* (1881), mistakenly, and carelessly also citing the basionym as *Gaylussacia cordata* Mart. & Gal., Bull. Acad. Brux. 9:529. 1842. As a result, instead of establishing the intended and needed binomial in *Vaccinium*, Hemsley created an illegitimate name (Article 52 of the ICBN) that is to be rejected as nomenclaturally superfluous. When Hemsley published *Vaccinium cordifolium*, there would have been no obstacle to proposing the binomial *Vaccinium cordifolium* based on Martens and Galeotti's binomial, but after 1894 *Vaccinium cordifolium* Stapf had been published (Trans. Linnean Soc. Ser. II. 4:189. 1894) and therefore a combination based on Martens and Galeotti's binomial would have resulted in a later homonym. However, when querried on this problem, three very experienced and knowledgable nomenclaturalists (Drs. J. McNeill, G. Moore, and D. Nicolson) all agreed that Hemsley's carelessness in transfering *Gaylussacia cordifolium* M.Martens & Galeotti into *Vaccinium* as *V. cordatum* (M.Martens & Galeotti) Hemsley, while also mistakenly citing the basionym as *G. cordatum,* should nevertheless be treated as a correctable error rather than as the publication of a later invalid synonym that Lundell corrected by publishing a new name since by that time *Vaccinium cordifolium* Stapf had been published for a species from Borneo. Consequently, the American species will be known as *V. cordifolium* (M.Martens & Galeotti) Hemsley as originally intended, while the Borneoan plant is provided with a binomial in the footnote below[1].

Additional collections examined: **MEXICO. Veracruz:** Municipio de Las Vigas; en las faldas del Volcancillo, por la carretera federal Jalapa-Las Vigas, 19°38'N, 97°03'W, 2000 m, 16 Aug 1979, *Calzada 5483* (F); Las Vegas, *Linden 420* (MICH); bosque de piño, 2300 m, El Volcancillo, 2300 m, 21 Jan 1976, *Ortega et al. 114* (F, NY). **Oaxaca:** wet hardwood montane forest, Hwy. 175 ca. 31 mi N of Ixtlán de Juarez, 7500 ft, 20 Dec 1972, *Almeda & Luteyn 1675* (DUKE). **Chiapas:** evergreen cloud forest on the N and W slopes of Cerro Mozotal below the microwave tower along the road from Huixtla to El Porvenir and Siltepec, 3000 m, 30 Dec 1972, *Breedlove & Thorne 31178* (DS, DUKE, MICH, MO, NY, RSA); Niquivil, Municipio de Motozintla, 2786 m, 15 May 1945, *Matuda 5497* (DS, LL, MICH). **GUATEMALA. Huehuetenango:** Sierra de Cuchumatanes, on slope with *Pinus*, *Quercus* and *Drimys*, 6 mi N of Santa Eulalia along road to San Mateo Ixtatán, 9200 ft, 5 Feb 1965, *Breedlove 8593* (DS, F); top of Cerro Chemalito, 3.5 mi W of Santa Eulalia, 3100–3150 m, *Steyermark 49946* (F, NY).

8. Vaccinium breedlovei L.O. Williams, Fieldiana Bot. 31:173. 1965. Type: GUATEMALA. Huehuetenango: Sierra de los Cuchumatanes, 6 mi N of Santa Eulalia along road to Santa Eulalia, 2800 m, Feb 1965 (fl), *Breedlove 8594* (holotype: F! photo NY neg. 9247; isotype: DS!).

Vaccinium tolbertianum Lundell, Wrightia 5:87. 1975. Type: GUATEMALA. El Quiché: El Boquerón in mossy secondary thickets, 8000–8200 ft, 10 Aug 1964 (im fr), *Proctor 25479* (holotype: LL! isotype: LL!).

Epiphytic *shrubs*; branchlets irregularly angled to ± terete, glabrous, reddish-brown. *Leaf-blades* persistent, coriaceous, evergreen, ovate to ovate-lanceolate, 5–15 cm long, 2.5–8 cm broad, apically acuminate to acute or rarely even rounded, basally rounded, marginally very finely but distinctly and minutely glandular crenate with the teeth 6–9 mm apart, glabrous on both surfaces, the venation pinnate, prominent on both surfaces and pronouncedly elevated thru the third order of branching forming a conspicuous reticulum, the midrib depressed into the upper surface forming a channel; petioles stout, 4–11 mm long, puberulous. *Inflorescences* axillary or arising from leafless nodes, racemose or paniculate (2–4 branches), often pronouncedly secund, 10–20-flowered, glabrous throughout; rachises 3–7 cm long; floral bracts scale-like, triangular to narrowly deltoid, 1–1.5 mm long, glabrous; pedicels slender, (5–)7–9 mm long, glabrous; bracteoles medially or more

[1]The species from Borneo, rendered by the above interpretation a later homonym is here named Vaccinium beamanianum Wilbur & Luteyn, nom. nov. based on *V. cordifolium* Stapf (Trans. Linnean Soc. Ser. II. 4:189. 1894). The specific epithet recognizes Professor John H. Beaman, a native of the mountains of western North Carolina, for decades an outstanding professor at Michigan State University, who has devoted recent decades to making better known the flora of Borneo.

distally attached, narrowly triangular to linear-lanceolate, 1.5–2 m long. *Flowers* 5-merous; calyx ca. 3–4 mm long, articulate with pedicel, the tube campanulate, terete, slightly constricted near summit, ca. 1.5–2.2 mm long and 2 mm in diam., glabrous, the limb somewhat flaring, the lobes rounded to somewhat deltoid to triangular, usually abruptly acuminate, ca. 1–1.5 mm long, glabrous; corolla with aestivation weakly imbricate, membranous, unistratose, broadly funnelform, strongly 5-angulate with pronounced medial nerves, 5–6 mm long, flaring distally to 6–7 mm in diam., glabrous, greenish to greenish-white often suffused with maroon, the lobes triangular, 2–2.5 mm long; stamens 10, included, ca. 5–5.5 mm long, the filaments ca. 3 mm long, glabrous, the anthers ca. 3 mm long, lacking spurs, the thecae ca. 2 mm long, papillate, the tubules ca. 0.8–1.5 mm long and 0.2 mm in diam., dehiscing by terminal, obliquely slanting pores; ovary 10-locular (?); styles ca. 5 mm long. *Berry* not seen.

Distribution.—Known only from four collections on forested slopes of pine, oak, and *Cupressus*, from Chiapas (Mexico) and Lempira (Honduras), at ca. 2300–2670 m. Flowering: Dec–Feb.

Vaccinium breedlovei is characterized by large (to 15 × 8 cm), glabrous leaves that are finely crenate margined and prominently, reticulately and pinnately veined, racemose to paniculate inflorescences, a calyx that is articulate with the pedicel, anthers lacking spurs, a greenish corolla, and possibly falsely 10-locular ovaries (mature fruits are needed). Although unable to make better suggestions as to the closest relatives of the very distinctive *Vaccinium breedlovei*, we do not see the close relationships with *V. poasanum* and the relatives of that species (sect. *Leptothamnia* Benth. & Hook.f.) as originally suggested by Williams. The inflorescence pattern would seem to argue against any close relationship with species centered around *V. poasanum*, although the stamens do suggest such a relationship.

Vaccinium tolbertianum Lundell was named from perhaps two incomplete collections made by the same collector at about the same time and place in Guatemala. The specimens (both LL) consisted of attached leaves, stems, and young fruits. The most unusual feature was the presence of coarse, stiff, rigid trichomes on a few centimeters of older stem on two of the six sprigs and on a few nearby leaves. Nothing like those trichomes has been seen in Meso-American vaccinia, but they are frequent in the genus *Gaultheria*. Other than for the presence of these gland-tipped trichomes, the specimens would fit reasonably well within the current concept of *V. haematinum* Standley & Steyermark. It seems they can still be best placed there in spite of the presence of those unique trichomes. Obviously further collecting may change our understanding of this little known variant. Specimens with flowers and trichome-bearing stems are unknown and it seems reasonable to conclude that without the presence of those coarse trichomes on a few centimeters of certain of the older branchlets, the species never would have been proposed.

Additional collection examined: **MEXICO. Chiapas:** broad ridge with evergreen cloud forest on the third ridge along logging road from Las Margaritas to Campo Alegre, 2300 m, 8 Dec 1986, *Breedlove & Mally 66262* (CAS). **HONDURAS. Lempira:** Montaña de Celaque, S of Río Arágual, 2670 m, 29 May 1991, *Davidse 34869* (MO).

9. Vaccinium chihuahuense Wilbur & Luteyn, sp. nov. (**Fig. 1**). Type: MEXICO. Chihuahua: Mojarachic, 1 Jun 1939, *Knobloch 5791* (holotype: US! photo NY neg. 13031; isotype: MSU! NY frag. ex US!).

Vaccinium lepidum Camp, ined. in herb.

Frutex. Rami pilosuli vel glabrati; ramuli pilosuli, tereti. Folia ut videtur persistens, elliptica, 10–15 mm longi et 3–8 mm lati, crenulato-serrulati, pilosulosi vel puburuli utrinque; petiole 1–2 mm longi, pilosuli. Inflorescentia racemosa, axilaria, 4–9 mm longa; rhachis puberulenta; bractae et bracteolae caducae, 1–2 mm longae; pediceli 1.5–4.5 mm longi, puberulenti. Caylx pedicellis articulatus, ca. 3.2–3.5 mm longus; tubi puberulenti; limbi calycis (0.8–)2–2.4 mm longi et 1.5–2 mm diam., puberulenti; lobi calycis 5, acuti, acuminati, erecti, ca. 1–1.9 mm longi et 0.8 mm lata basi, puberulenta; corolla alba vel carnea, 3.5–5 mm longi and 2–2.5 mm diam., pilosulosi; lobi corollae ca. 1 mm longi, erecti, oblongi.

Terrestrial *shrubs*, 0.8–1.3 m tall; mature branchlets terete, striate, moderately to densely pilosulose with the hyaline trichomes ± spreading at right angles to the stem's surface branchlets, to even glabrate, the bark thin, grayish to brownish, splitting longitudinally and exfoliolating; twigs sharply and narrowly angled, striate, moderately to densely pilosulose. *Leaves* apparently persistent, coriaceous, evergreen, the blades flat to concave, elliptic to ovate-elliptic, 10–15 mm long, 3–8 mm broad, apically acute to broadly rounded,

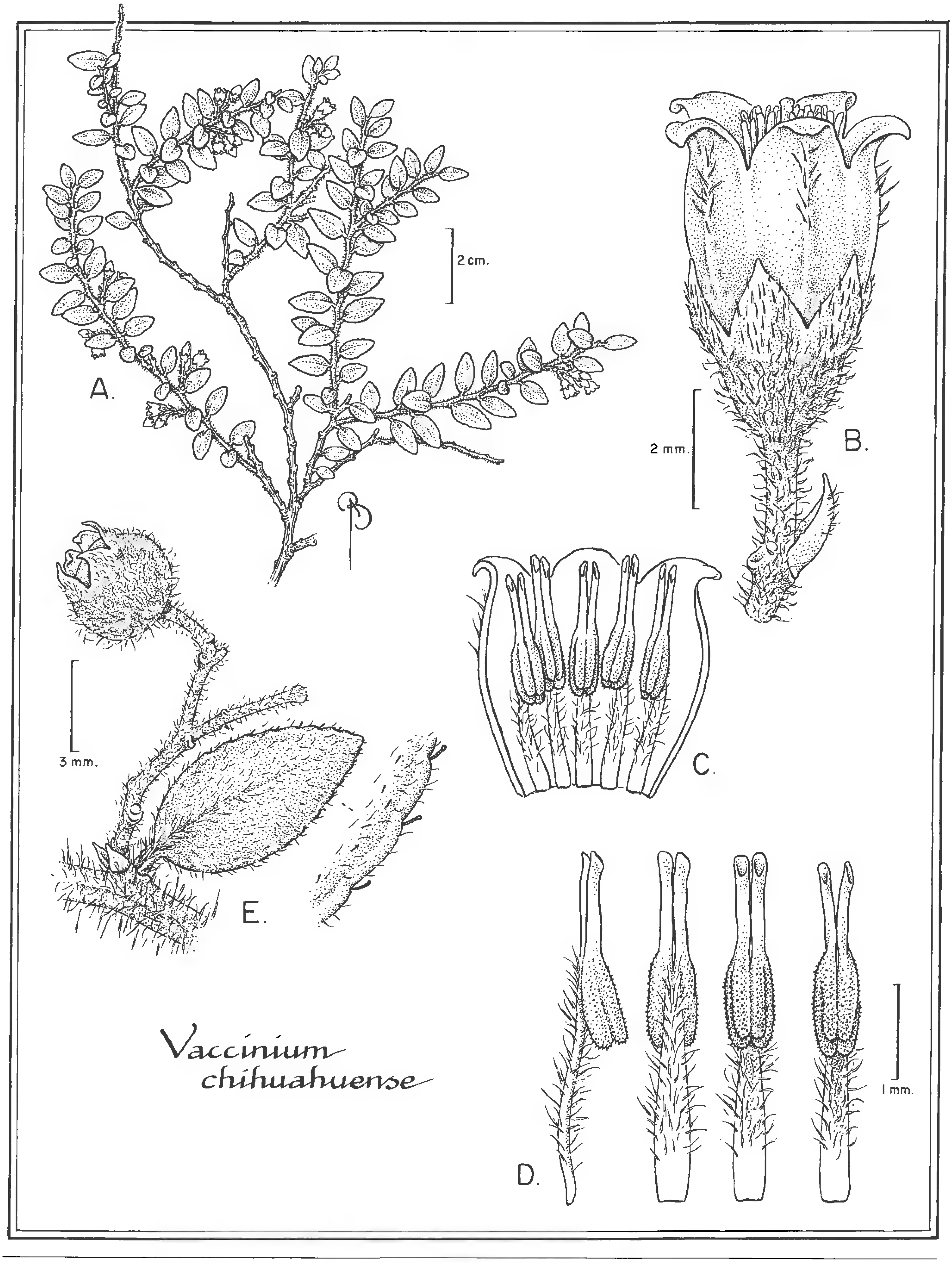

Fig. 1. *Vaccinium chihuahuense* Wilbur & Luteyn. A, habit. B, flower showing pubescence. C, corolla opened to show orientation of 5 stamens. D, stamens showing side, ventral, and two dorsal views with introrse, oblique dehiscence pores. E, portion of stem showing leaf, old inflorescence, and immature fruit, with inset showing crenate leaf margin (drawn from type collection).

basally cuneately tapering to broadly rounded, marginally indistinctly crenulate-serrulate with the teeth terminating in a reddish, gland-tipped vein extension (glandular fimbriae), both surfaces densely puberulent or pilosulose with hyaline, spreading trichomes, the lower surface deciduously glandular-fimbriate, the venation pinnate, inconspicuous to conspicuous above, the midrib impressed above and raised beneath, the secondary and tertiary venation impressed above; petioles somewhat flattened and canaliculate above, 1–2 mm long, densely pilosulose. *Inflorescences* axillary, racemose, 2–8-flowered; rachises ca. 4–9 mm long, moderately short-puberulent; floral bracts and bracteoles caducous, oblong, acute to obtuse, 1–2 mm long, ± glabrous; pedicels 1.5–4.5 mm long, densely puberulent. *Flowers* 5-merous; calyx ca. 3.2–3.5 mm long, articulate with pedicel, the tube ca. 1–1.5 mm long, ca. 1 mm in diam., moderately to densely puberulent, the limb (0.8–)2–2.4 mm long, densely puberulent, the lobes erect, narrowly triangular to ovate, acute to shortly acuminate, ca. 1–1.9 mm long, ca. 0.8 mm broad at base, puberulent; sinuses acute; corolla with aestivation imbricate, membranous, unistratose, cylindric, angled opposite the lobes, 3.5–5 mm long, ca. 2–2.5 m in diam., whitish-pink, externally sparingly to moderately pilosulose especially distally along angles, the lobes erect, oblongish, roundedly acute, ca. 1 mm long; stamens 10, included, ca. 2.7 mm long, the filaments ca. 1.7–1.8 mm long, pilosulosely ciliate to densely pilosulose, the anthers ca. 1.5 mm long, lacking spurs, the thecae ca. 0.5–0.7 mm long, ± smooth, the tubules distinct, ca. 0.8–1 mm long, dehiscing by introrse, oblique, tear-shaped pores; styles glabrous, ca. 4–5.5 mm long. *Berry* not seen.

Distribution.—Known only from several collections in forest of *Quercus-Pinus* with thin, rocky, litosol soils, from the state of Chihuahua, Mexico, at 1950–2200 m. Flowering: Jun–Aug; fruiting: Oct.

Vaccinium chihuahuense is characterized by having persistent pubescence in nearly all parts, small leaves that are marginally crenate-serrulate, an articulate calyx, anthers that lack spurs. Morphologically it resembles *V. confertum*, from which it differs most conspicuously in its persistent, dense pubescence of all vegetative and floral parts.

Additional collections examined: **MEXICO. Chihuahua:** Mojarachic, Jan 1937 (st), *Knobloch 5736* (MSU); Parque Nacional Cascada de Basaseachic, Mpio. de Ocampo, 2200 m, 12 Mar 1994 (st), *Garcia et al. 2527* (NY), 2100 m, 3 Oct 1986 (im fr), *Spellenberg et al. 8701* (NMC), 1950 m, 5Aug 1994 (fl), *Yen & Estrada 2841* (DUKE, NMC, NY); Divisadero Overlook of Cascada de Basaseachic, 2100 m, 23 Jun 1987 (fl), *T. R. Van Devender et al. 87-160* (NMC); Mpio. de Guachochic, Cascada de Cusarare, 28 Jul 1973 (fl), *Bye 4400* (NMC).

10. Vaccinium lundellianum L.O. Williams, Fieldiana Bot. 31:173. 1965. (Based on *Malea pilosa* Lundell, non *Vaccinium pilosum* A. Chevalier ex Dop., 1930).

Malea pilosa Lundell, Amer. Midl. Naturalist 29:484. 1943. Type: MEXICO. Chiapas: Mt. Malé, near Porvenir, 3200 m, 6–12 Jul 1941, *Matuda 4614* (holotype: MICH!; isotypes: A! photo NY neg. 9675, CAS! LL! NY! photo NY neg. 9632).

Epiphytic *shrubs*; branchlets terete, ± blackish, ± pilosulose throughout with whitish trichomes. *Leaf-blades* persistent, coriaceous, evergreen, oblong to lance-oblong or even lanceolate, 3–4.5(–7.5) cm long, 0.8–2(–3) cm broad, apically obtuse to subacute, basally usually rounded, marginally entire or nearly so, occasionally with a few, remote glandular teeth, somewhat shiny above and dull beneath, persistently pilose beneath and puberulent or pilosulose above at first but glabrescent with age, the venation pinnate, visibly reticulate on both surfaces with the midrib and primary veins elevated; petioles ridged and grooved, 2.5–8 mm long, densely pilosulose. *Inflorescences* axillary, solitary, racemose, congested, ca. 2–6-flowered; rachises subsessile, mostly 2–5 mm long, densely pilosulose, bearing small, imbricate bracts at base; floral bracts persistent, deltoid, ca. 1–1.2 mm long, pilosulose; pedicels slender, 3–7 mm long, pilosulose; bracteoles persistent, basal or attached below the middle, opposite to subopposite, lanceolate to linear, 1.5–1.6 mm long. *Flowers* 5-merous; calyx ca. 3–3.3 mm long, sharply articulate with pedicel, the tube subcampanulate to ± globose, ca. 1.5 mm long, densely pilosulose, the lobes narrowly deltoid, acute, ca. 1.3–1.7 mm long; corolla with aestivation imbricate, membranous, unistratose, subcylindric, pentagonal, slightly swelling above, 8–10 mm long, white, pilosulose externally, the lobes erect or nearly so, obtuse, 2–3 mm long; stamens 10, included, 8.5–9.6 mm long, the filaments 6.3–7.2 mm long, pilosulose, at the base weakly attached to corolla, attached to the anthers dorsally near the middle, the anthers ca. 3.5–4 mm long, lacking spurs, the thecae ca. 2–2.3 mm long including the attenuate base, the tubules slender, ca. 1.6–2 mm long, dehiscing

by introrse clefts; styles slightly exserted. *Berry* spherical, at least 4 mm diam. when immature, pilosulose, glabrate, falsely 10-locular.

Distribution.—Known only in cloud forests, from a few collections from the Mexican state of Chiapas and the Guatemalan states of Huehuetenango and San Marcos, between 2000–3000 m. Flowering:Jul; fruiting: immature Jan.

Vaccinium lundellianum is characterized by its oblong to lanceolate, entire-margined and pilose leaves to 4.5(–7.5) cm long, congested racemes, pilosulose inflorescences (including the rachis, pedicel, calyx, corolla, and fruit), relatively long corollas (8–10 mm long), and a falsely 10-locular berry.

Additional collections examined: **MEXICO. Chiapas:** steep slopes with evergreen cloud forest, NW slope of Cerro Malé, 3–4 km W of El Porvenir along road from Huixtla to Siltepec, 19 Sep 1976, *Breedlove 40381* (F, CAS, MO, NY, RSA, TEX); sobre arboles altos, Rodeo-Siltepec, 2000 m, 29 Apr 1964, *Matuda 37378* (F, MO). **GUATEMALA. Huehuetenango:** Sierra de los Cuchumatanes, La Sierra (Tujimach), across river from San Juan Atitán, 2500–2900 m, upper forested slopes, 8 Sep 1942, *Steyermark 52017* (F). **San Marcos:** montane cloud forest area on outer slopes of Tajumulco Volcano, ca. 8–10 km W of San Marcos, ca. 2300 m, 31 Dec 1964, *Williams et al. 26886* (F, NY). **HONDURAS. Atlantida:** Pico Bonito National Park, 2435 m, *T. Hawkins 920* (MO).

11. Vaccinium selerianum (Loes.) Sleumer, Notizbl. Bot. Gart. Berlin-Dahlem 13(116):124. 1936. *Pernettya seleriana* Loes., Bull. Herb. Boiss. ser. II. 3:217. 1903. Type: MEXICO. Chiapas: "in distr. del Centro," in silva montaña inter San Cristóbal Las Casas et Huitzán," 10 Mar 1896, *Seler & Seler 2126a* (holotype: B†, photo F neg. 4597; isotype: GH!, photo NY neg. 11118).

Vaccinium haematinum Standley & Steyermark, Field Mus. Nat. Hist., Bot. Ser. 23:139. 1944. Type: GUATEMALA. Huehuetenango: Cerro Huitz, between Mimanhuitz and Yulhitz, Sierra de Cuchumatanes, 1500–2600 m, 14 Jul 1942, *Steyermark 48572* (holotype: F! photo F neg. 52552 and NY neg. 9656).

Vaccinium minarum Standley & Steyermark, Field Mus. Nat. Hist., Bot. Ser. 23:219. 1947. Type: GUATEMALA. Zacapa: middle and upper southern slopes of Volcán Gemelos, Sierra de las Minas, 2100–3200 m, 26 Jan 1942, *Steyermark 43295* (holotype: F! photo F neg. 52553 and NY neg. 9657; isotype: US! photo NY neg. 11119).

Vaccinium hondurense A.C. Smith, Ceiba 3:185. 1953. Type: HONDURAS. Morazán: San Juancito Mts., ca. 6 km W of San Juancito, Rancho Quemado on rotting stumps in rain forest, 2100 m, 8 Jul 1852 [1952], *L.O. Williams 18567* (holotype: US! photo NY neg. 9443; isotypes: DS! F! GH!).

Vaccinium quicheanum Lundell, Wrightia 5:86. 1975. Type: GUATEMALA. El Quiché: Nebaj, 8000 ft, in pineland, 13 Jun 1964, *Contreras 4983* (holotype: LL!).

Epiphytic or terrestrial, bushy *shrubs* or rarely small *trees* (0.5–)1–3(–4.5) m tall; branchlets ridged and grooved and somewhat angular to nearly terete, when young often reddish but becoming brown or even blackish-brown in age, at first glabrous to more typically moderately to even densely puberulent and then later becoming glabrate. *Leaves* often numerous and overlapping, the blades persistent, coriaceous, evergreen, narrowly to broadly elliptic to oblong-elliptic or even obovate-oblong to even lanceolate, 2–4.5(–6.5) cm long, (0.8–)1.2–2.5(–5) cm broad, apically acute to obtuse or even broadly rounded to tapering to an ultimately obtuse apex, basally rounded to acutely cuneate, marginally remotely and inconspicuously to conspicuously crenate-serrulate, often lustrous especially above, glabrous or nearly so on both surfaces to moderately although inconspicuously and finely puberulent to pilosulose, the venation pinnate, the midrib flush above or basally somewhat elevated but mostly somewhat channeled while beneath ± elevated, the lateral veins above ± flush with the surface while beneath either flush or elevated and often conspicuously so and then forming a reticulum; petioles subterete, often canaliculate above, rugose, 1.5–5 mm long, glabrous or puberulent to short-pilose. *Inflorescences* axillary, racemose, 6–12-flowered; peduncles and rachises together 3–12 mm long, sparsely to moderately puberulous; floral bracts caducous to deciduous, narrowly triangular to oblongish, often concave, (1.5–)2–7 mm long, shortly ciliate, ± scarious, externally glabrous or medially ciliate; pedicels reflexed or turned downwards, 1.5–5(–9) mm long, puberulent; bracteoles medially to distally placed, alternate, appressed, caducous to deciduous, broadly elliptic to lanceolate, 2–3.5 mm long, sparingly indistinctly ciliate, occasionally externally medially short-pilose. *Flowers* 5-merous; calyx 3–4.5 mm long, conspicuously articulate with pedicel, the tube spherical to oblong-cylindric, 1.5–2.2 mm long, glabrous to densely puberulent or pilosulose, the lobes deltoid to narrowly triangular, acute, (0.8–)1.2–1.8 mm long, externally and internally glabrous to externally moderately puberulent to pilosulose, marginally glabrous to minutely ciliate and often sparingly and inconspiciously glandular; corolla with aestivation imbricate,

membranous, unistratose, cylindric, 5–7.2(–9) mm long, ca. 3 mm in diam., deep rose to pinkish or white, glabrous both externally and internally or moderately to densely pilosulose externally, the lobes broadly oblong to deltoid, obtuse to acute, ca. 1–2 mm long; stamens 10(–12), included, 3.7–7(–7.7) mm long, the filaments 2.3–5(–5.7) mm long, attached dorsally to the lower third or half of the anther, flattened, densely ciliate, the anthers 1.8–4 mm long, lacking spurs, the thecae ca. 1.3–2.2 mm long, minutely papillose, the tubules slender 0.7–2.2 mm long, dehiscing by short, oblique pores or short clefts. *Berry* terete, 5–9 mm diam., reddish during maturation but apparently blackish at maturity, glabrate to sparingly pilosulose, 4–5-locular.

Distribution.—Oak forests, evergreen cloud forests, and mossy thickets, in southern Mexico (Oaxaca and Chiapas), south through Guatemala (El Quiché, Huehuetenango, and Zacapa) into Honduras (Lempira and Morazán) and El Salvador (Santa Ana), from 1600–3200(–3700) m. Flowering: (Jan)May–Aug(Dec); fruiting: throughout the year.

Vaccinium selerianum is a morphologically variable species characterized by its congested leaves that are elliptic to oblong-elliptic to lanceolate, 2–4.5 cm long, with margins crenate-serrate, short-racemose inflorescences, an articulate calyx, glabrous to pilose corollas, anthers that lack spurs, and a 4–5-locular ovary.

Recently, as exemplified by the treatment in the *Flora of Guatemala* (L.O. Williams *in* Standley & Williams 1966), two species have been recognized within what is treated here as a single species of *Vaccinium*. They are separated there by the following straightforward couplet:

Flowers glabrous __________ **V. haematinum**
Flowers densely pubescent __________ **V. minarum**

The brief descriptions there indicate that the calyces of *V. haematinum* vary from "sparsely and minutely puberulent or glabrate." Specimens have been examined with glabrous or at least glabrate calyces and pilosulose corollas. The leaves and vegetative features of both "species" seem to have the same range of variation. It cannot be claimed that a morphological continuum exists between the two extremes, but the variation exhibited by the small sample available suggests that a much larger sample would in all probability further blur the supposed distinctions between the named extremes. It seems that only one, not extremely polymorphic species is represented. The extremes in pubescence of the calyx seem to be rather widely bridged, but there seems to be no similar blurring in corolla pubescense; those previously assigned to *V. minarum* have densely pubescent corollas while those attributable to *V. haematium* are glabrous.

The flowers on the type specimens of *V. minarum*, *V. quicheanum*, and *V. hondurense* are exactly similar as to pubescence, although the leaves of *V. quicheanum* are more elongate, while those of *V. minarum* are smaller and narrower. As far as the long list of names is concerned, *V. selerianum* (Loes.) Sleumer (1936) has priority.

Additional collections examined: **MEXICO. Oaxaca:** dry wooded slopes and ravines surrounding Llano Verde ca. 12 km ESE of Ixtlán de Juarez, 17°18'N, 96°22'W, 2000–2400 m, 6 Jun 1970, *Graham & Frohlich 1101* (MICH); vicinity of Cerro Zempoaltepetl, openings of *Cupressus-Pinus* woodland, ca. 5 km E of summit, 2800 m, 9 Aug 1950, *Hallberg 884* (MICH); rainforest along road between Ixtlán and Valle Nacional, just below summit at Cerro Pilón, 17°35'N, 96°30'W, ca. 8000 ft, 20 Jun 1969, *Webster & Breckon 15350* (GH). **Chiapas:** steep forested slopes on the SE side of Cerro Tres Picos and the ridges near summit, 2100–2500 m, 28 May 1972, *Breedlove 25443* (DS, DUKE, MICH, MO, NY, RSA); evergreen cloud forest along logging road from Las Margaritas to Campo Alegre, 2300 m, 24 Oct 1976, *Breedlove 41099* (DS, MICH, MO). **GUATEMALA. El Quiché:** El Boquerón; in mossy cloud forest, 8000–8200 ft, *Proctor 25435* (MO). **Huehuetenango:** Sierra de los Cuchumatanes, near small stream in pine forest between Km 324 & 325 on Ruta Nacional 9N between Chemal and San Juan Ixcoy, 3140 m, 4 Aug 1959, *Beaman 3051* (MSC); steep rocky slopes along road to San Juan Ixcoy, 3700 m, 12–23 Jan 1966, *Molina et al. 16438a* (F, NY, US). **Zacapa:** on summit between Loma El Picacho and Cerro de Moños, 2000–2600 m, 16 Jan 1942, *Steyermark 42836* (F, US). **HONDURAS. Lempira:** Sierra de Celaque, encima de un filo, 2750 m, 18–22 Nov 1974, *Hazlett 2262* (F, MO). **Morazán:** frecuente en la floresta humeda y nebulosa de Montaña La Tigra, entre El Piliguin y Prado de Fatima, 1800 m, 30 Dec 1962, *Molina R. 11217* (F, LL, NY, US). **EL SALVADOR. Santa Ana:** bosque nebulosa, de Montaña Montecristo, 2300 m, 23 May 1963, *Molina R.. 12683* (F, LL, NY, US).

12. Vaccinium talamancense (Wilbur& Luteyn) Luteyn, Brittonia 53:444. 2001. *Macleania talamancensis* Wilbur

& Luteyn, Brittonia 29:263, fig.3. 1977. TYPE: COSTA RICA. SAN JOSÉ: along trail from Canaan to Chirripó via Los Angeles, N of Río Talari, 3200–3400 m, 19–22 Jan 1970, *Burger & Leisner 7401* (HOLOTYPE: DUKE!; ISOTYPES: F! MO! NY!).

Terrestrial *shrubs*, 0.5–1 m tall; mature branchlets terete, striate, glabrous; twigs subterete, bluntly and broadly compressed, puberulent to densely short-pilose, glabrate. *Leaves* imbricate, the blades persistent, coriaceous, evergreen, obovate to more typically oblong-elliptic, 2.5–4.7 cm long, 1.2–1.8(–2.3) cm broad, apically acute or rounded but with a 1–2 mm long apiculus, basally rounded, marginally indistinctly and minutely serrulate, the actual margin a lighter color and seemingly a bit thinner than lamina proper, essentially glabrous above except finely whitish, appressed-pilosulous near the base along midrib and inconspicuously ciliate especially proximally, indistinctly and sparingly whitish, appressed-pilosulous beneath basally and also bearing appressed, reddish-brown, glandular-fimbriae ±0.2 mm long, provided with 1–2 reddish, circular basal glands, the venation pinnate with 3–4 arcuate-ascending lateral nerves per side, the midrib slightly thickened and raised proximally but impressed distally, lateral nerves impressed above, all veins prominently elevated beneath and of a lighter color than lamina proper; petioles thick, flattened or broadly canaliculated above and slightly winged throughout, rugose, 2–3 mm long, moderately puberulous to short-pilose. *Inflorescences* axillary, racemose, 10–15-flowered; rachises strongly and sharply angled, 1–2(–4) cm long, pilose with soft, short, white trichomes; floral bracts appressed, linear to lanceolate 3–4 mm long, puberulent; pedicels 6–10 mm long, softly pilosulous or puberulous, bearing distally a series of glandular fimbriae; bracteoles basal, appressed, linear to narrowly lanceolate, 2–3 mm long, puberulent, marginally glandular-fimbriate, without dorsal glands. *Flowers* 5-merous; calyx 4.5–5 mm long, articulate with pedicel, the tube campanulate to cylindric, ca. 2.5–3 mm long and in diam., longer than limb, moderately puberulous with whitish trichomes ±0.1–0.2 mm long, the lobes triangular, acute, 1.2–1.8 mm long, puberulous externally and internally; corolla with aestivation apparently valvate, membranous, weakly bistratose, cylindric, terete, 8–13 mm long, 4–6 mm broad, pink to red, appressed- to spreading-puberulous externally with moderately abundant hyaline trichomes ± 0.4 mm long, moderately to densely pilose with hyaline trichomes within, the lobes strongly reflexed, triangular, 1.5–2 mm long, pink to red although sometimes becoming pale pink to whitish, densely pilosulous both externally and internally; stamens 10, included, 7–7.5 mm long, the filaments 3.5–4 mm long, glabrous proximally but marginally with appressed-pilosulous hyaline trichomes distally, the anthers 4.5–5 mm long, lacking spurs, the thecae 1.8–2 mm long, smooth, basally strongly incurved, the tubules 2.5–2.7 mm long, dehiscing by oblique pores ca. 0.6 mm long; styles exserted. *Berry* spherical, 8–10 mm diam., blue-black, short-pilose, 5-locular.

Distribution.—Known only in upper oak forests and disturbed páramo habitats, from the upper slopes of Cerro Chirripó, from ca. 2500–3819 m. Flowering: Jan, Mar–Apr; fruiting: Dec, Mar–Apr.

Vaccinium talamancense is characterized by its leaves with blade margins indistinctly and minutely serrulate, red to pink corollas that are appressed- to spreading-puberulous externally and moderately to densely pilose internally, anther connectives that lack spurs, and a pilose berry that is not glaucous. Its interspecific relationships are uncertain at this time.

Additional collections examined: **COSTA RICA. San José:** Cordillera de Talamanca, Cerro Chirripó massif; forest just below the páramo with many dead trees and many ericaceous shrubs, 3200 m, *Davidse & Pohl 1594* (DUKE, MO); Parque Nacional Chirripó, Cuenca Térraba-Sierpe, base of Cerro Crestones, 3460 m, 7 Dec 1996 (fr), *Alfaro 1011* (MO); Pacific slope, trail to Cerro Urán, 3000 m, 7 Apr 1995 (fl), *González 662* (INB); sendero de las Machinas, Monte Sin Fe, 2590 m, 18 Mar 1999 (fl, fr), *Luteyn & Chaverri 15415* (CR, INB, NY); trail beyond Río Talari to Valle de Los Leones, 3200–3300 m, 20 Mar 1999 (fl, fr), *Luteyn & Chaverri15430* (AAU, CAS, CR, DUKE, F, INB, K, MEXU, MO, NY, TEX, US); Sabana de Los Leones, Cerro Lohmann, 3200 m, 26 Jan 1996 (fl), *Morales 5177* (F, INB, NY); between La Piedra and lower refugio, 17–28 Mar 1976 (fl), *Weston 10134* (CR).

13. Vaccinium floribundum Kunth in H.B.K., Nov. Gen. Sp. Pl. 3:266, t. 251. 1818. TYPE: PERU. AMAZONAS: "Crescit in montanis Peruviae, prope Carxamarca, alt. 1700 hex. Floret Augusto," *Humboldt & Bonpland* s.n. (HOLOTYPE: P-HBK! ISOTYPES: B-Willd. 7353-1! P!).

Densely branched, terrestrial *shrubs* 2–8(–12) dm tall, sometimes arising from lignotubers to 10 cm in diam.; branchlets few, angled to terete, glabrous or puberulent. *Leaf-blades* persistent, coriaceous, evergreen,

highly variable in shape and size from very broadly ovate or nearly orbicular to elliptical or ovate-oblong, 0.4–1.5(–2.5) cm long, 0.3–1.2 cm broad, apically acute to obtuse, basally rounded to somewhat cuneate, marginally thickened and ± revolute and shallowly crenate-serrulate, occasionally inconspicuously and sparingly spreading pilosulose above and this pubescence more abundant basally and ± glabrate except for the moderate to dense puberulence along the midrib, the lower surface glabrous to moderately beset with appressed to somewhat ascendent, glandular trichomes and these appearing as punctate dots as the trichomes drop away, the venation pinnate; petioles flattened above, 2–3(–4) mm long, very shortly puberulent. *Inflorescences* axillary, racemose (very rarely weakly paniculate), 6–10-flowered; rachises strongly angulate, 1–2(–4.5) cm long, puberulent to glabrous or very nearly so; floral bracts broadly ovate to oblong, 2.5–4.5 mm long, (2–)3–4.5(–5.5) mm broad, minutely appressed puberulent on the abaxial surface to nearly glabrous, minutely ciliate and occasionally glandularly ciliate; pedicels 3–4(–6) mm long, usually spreading puberulous but occasionally glabrate; bracteoles medially to basally attached, ± ovate to lance-ovate or even narrowly lunear-oblong, 2.5–4.8 mm long, 1.5–2.5 mm broad slightly appressed puberulous externally to glabrate, marginally minutely ciliate and occasionally also slightly glandular-ciliate. *Flowers* 4–5-merous; calyx ca. 3–4 mm long, sharply articulate with pedicel, the tube campanulate to short-cylindric, 1.5–1.8 mm long, 1.2–1.8 mm in diam., glabrous, the lobes deltoid to ovate-oblong, acute, ca. 1–1.5 mm long, glabrous, usually ciliate; corolla with aestivation imbricate, membranous, unistratose, cylindric, 5–6.5 mm long, 2–3 mm in diam., white to roseate, glabrous, the lobes ± erect, deltoid, acute, ca. 1.5 mm long, glabrous; stamens 8 or 10, included, 3.8–6 mm long, the filaments 2–2.5 mm long, flattened, densely spreading ciliate with hyaline trichomes, the anthers 2.5–3.5 mm long, lacking spurs, the thecae 1–1.5 mm long, densely papillate or sharply and minutely spinulose, the tubules 1.5–2 mm long, dehiscing by introrse, oblique pores. *Berry* spherical, ca. 4–6 mm in diam., dark bluish-black, sometimes reddish when immature, 4–5-locular.

Distribution.—Disjunct from the South American Andes. Mossy thickets of the highest reaches of the Talamancas of Costa Rica, at 1400–3450 m. Flowering: Feb–Apr, Oct; fruiting: Feb–Mar.

Vaccinium floribundum is characterized by its small leaves the blades of which are pinnately nerved and minutely crenate-serrate margined, racemose inflorescences with small white to pink flowers, spurless connectives, and glaucous berries. In Costa Rica the stamens lack spurs, whereas populations in South America have at least vestigial spurs. *Vaccinium floribundum* is most closely related to *V. consanguineum*, as mentioned herein.

Additional collections examined: **COSTA RICA. San José:** Cerro de la Muerte, Cerro Sábila, 80 m N of summit, 3400 m, 28 Mar 1985, *Horn 131* (WIS); wet páramo thicket, Cerro de las Vueltas, 2700–3000 m, 1 Jan 1926, *Standley & Valerio 43697* (US); Buenavista Massif, summit of Cerro Sákira, 3417 m, 29 Aug 1969, *Weston 6005* (F); Parq. Nac. Chirripó, Valle de Los Conejos, 3500–3600 m, 19 Mar 1999, *Luteyn & Chaverri 15417* (AAU, CAS, INB, NSW, NY, STE, TEX). **Puntarenas:** páramo on the international border, Cerro Echandi, 9°02', 82°49'W, 3050–3160 m, 22 Aug 1983, *Davidse et al. 23856* (MO). **Limón:** Cordillera de Talamanca, Cerro Kamuk, 9°16'N, 83°02'30"W, 3200–3350 m, 24 Mar 1984, *Davidse et al. 25979* (MO).

14. Vaccinium confertum Kunth in H.B.K., Nov. Gen. Sp. Pl. 3:265, t. 250. 1818. Type: MEXICO. "prope Moran et Cerro de Oyamel, alt. 1400 hex," *Bonpland 4099* (holotype: P-HBK! frag. F! isotypes: B†, B-Willd. 8314-1! P!). The isotype in the Willdenow Herbarium has the label as "*Humboldt & Bonpland 4099*."

Vaccinium eriocladum Dunal, DC. Prodr. 7:571. 1839. *Vaccinium confertum* var. *eriocladum* (Dunal) Sleumer, Notizbl. Bot. Gart. Berlin 13:128. 1936. Type: MEXICO. Veracruz[?]: inter Tampico et Real del Monte, 20 May 1827, *Berlandier 254* (holotype: G-DC! photo NY s.n., frag. NY!; isotypes: B†, BM!, F!, OXF!, P(x4)!, W!). There are three sheets at P, one is incorrectly annotated as the holotype of *V. eriocladum* by Sleumer in 1958; it and another sheet at P both have the "ex. 12" written on the label too. Then there are two other *Berlandier 254* collections at P and one at OXF, none of which have the "ex. 12" on the label. All sheets are definitely *V. confertum*!

Vaccinium brachystachyum Benth., Pl. Hartweg. 65. 1840. Type: MEXICO. Oaxaca: "in montibus Carmen in jugo la Sierra dicto," *Hartweg 480* (holotype: K-Herb. Benth.!, frag. US!, photo NY neg. 11116; isotypes: CGE (x2)! K-Herb. Hook.! NY! OXF! P!).

Vaccinium discolor M.Martens & Galeotti, Bull. Acad. Brux. 9:531. 1842. Type: MEXICO: "sur les pics élevés de la cordilière orientale d'Oaxaca (Cerro de Capulalpan, Pelado de San Andres, etc.) , entre 7,500 et 9,500 pieds," *Galeotti 1818* (holotype: BR!; isotypes: BR, 2x! F! NY, 2x! P, 2x! US! photo NY neg. 11117, W! photo F neg. 31963). The labels on the *Galeotti 1818* isotype sheets at BR (one of them), F, NY, and US give "Oaxaca, Llano Verde" as the locality. Of the sheets at BR, the one labeled as "TYPUS" has the locality as "(Oaxaca) Sierra 7000"; another unannotated isotype has no locality data on its label, and the third isotype has "Oaxaca, Llano Verde."

Pernettya ovata Fernald, Proc. Amer. Acad. 36:496. 1901. Type: MEXICO. Chiapas: mountain woods between San Cristóbal Las Casas and Huitztlán, 10 Mar 1896, *Seler & Seler 2126b* (holotype: GH! photo NY s.n.).

Densely branched, terrestrial *shrubs*, 2–6(–10) dm tall; branchlets strongly ridged and grooved and hence appearing angulate, very densely puberulent or pilosulose to shortly hirsutulose (or reportedly very rarely glabrous). *Leaf-blades* persistent, thick-coriaceous, evergreen, oval to oblong-ovate, 6–15(–30) mm long, 4–10(–15) mm broad, apically acute to somewhat rounded, basally rounded, marginally finely but conspicuously crenate-serrulate, the upper surface finely and inconspicuously pilosulose to glabrate, deep green and shining while beneath pale and usually with scattered, inconspicuous, appressed, gland-tipped trichomes, the venation pinnate; petioles semicircular, canaliculate above 1–2(–3) mm long, puberulent to pilosulose. *Inflorescenses* axillary, densely compact, racemose, 3–7-flowered, almost always shorter than the subtending leaf; rachises mostly 8–12 mm long; floral bracts caducous, cuculate, oblong, ca. 2–4 mm long; pedicels (1–)2–3(–4) mm long, finely short-pubescent; bracteoles basal, caducous, cuculate, oblong, 1.2–1.5 mm long. *Flowers* 4–5-merous; calyx 3–3.3 mm long, conspicuously articulate with pedicel, the tube campanulate or globose, ca. 1–2 mm long and in diam. at anthesis but enlarging to ca. 3(–4) mm in diam. in fruit, glabrous, the lobes deltoid, acute, ca. 1–1.5 mm long; corolla with aestivation imbricate, membranous, unistratose, cylindric to weakly cylindric-campanulate or weakly cylindric-urceolate, 4–6.5 mm long, white to pinkish; stamens 10, included, 4.7–6.4 mm long, the filaments (1.5–)2.4–3.5 mm long, ciliate, the anthers 3.2–3.6 mm long, lacking spurs (or rarely bearing dorsally 2, minute, vestigial spurs), the thecae ca. (1–)1.4–2 mm long, the tubules ca. (1–)2–2.3 mm long. *Berry* 4–6 mm in diam., bluish or blackish with a glaucous bloom, 4–5-locular.

Distribution.—Montane forested slopes of pine-oak, rocky meadows, and clearings, from northern Mexico (Chihuahua, Tamaulipas, San Luis Potosi, Nayarit, Aguascalientes, Queretaro, Hidalgo, Vera Cruz, Puebla, Mexico, Jalisco, Guerrero, Oaxaca, and Chiapas), south into Guatemala (Chimaltenango, Huehuetenango, Quetzaltenango, San Marcos, Solola, and Totonicapan) and Honduras (Comayagua, Lempira, Olancho, and Ocotopequez), at 1538–4038 m. Flowering: throughout the year but especially in Jan–Jun; fruiting: throughout most of year but especially in Mar–Aug.

Vaccinium confertum is characterized by small, more or less concave leaves, 6–15 mm long (rarely to 30 mm long) with finely crenate-serrulate margins, densely compact racemose inflorescences of 3–7 flowers that are usually shorter than the subtending leaves, an articulate calyx, anthers that lack spurs (or are rarely vestigial), and a glaucous, 4–5-locular ovary. Its similarities with *V. chihuahuense* are mentioned above.

Additional representative collections examined: **MEXICO. Chihuahua:** pine-oak woods in mountains between Nabogame and Guadalupe and Calvo, 7200 ft, 12 Oct 1959, *Correll & Gentry 23048* (LL, NY); Sierra Madre, 15 mi E of Batopilas, 1–2 Oct 1898, *Goldman 183* (GH, US); Lagotera, 5–6000 ft, 21 Jul 1965, *Pennington 95* (TEX). **Tamaulipas:** large, loose rock formation near Rancho Gómez Farias, Apr 1960, *Duke M3543* (AAU, MO, NY). **San Luis Potosí:** San Luis Potosí, 6000–8000 ft, *Parry & Palmer 561* (F, GH, MO, NY, PH, US); Cerro Grande, 8 km al NW de Guadalcazar, 2100 m, 19 Jun 1955, *Rzedowski 5960* (F, MO, TEX). **Nayarit:** bosque en barranca, 1.5 km al S de Santa Teresa del Nayar, Municipio de Jesús Maria, 8 Jun 1978, *Diaz L. 9541* (MICH). **Aguascalientes:** Sierra del Laurel, near the Jalisco-Aguascalientes border, ca. 10 mi SE of Calvillo, oak forests near summits, 2500–2700 m, 26–28 Aug 1960, *McVaugh 18445* (MICH). **Queretaro:** ladera de cerro con bosque de coniferas, 2 km al SW de Pintal de Amoles, 2400 m, *Fernández 2710* (MO, NY). **Hidalgo:** bosque de pino y encino, alrededores de Zacualtipán, 1 Feb 1964, *Gonzales Q. 311* (DUKE, MICH, MSC, TEX); bosque de encino, 1.5 km al SSW de Tezuantla, 2950 m, 29 Jun 1975, *Medina 472* (CAS, NY). **Veracruz:** on old lava, La Joya, Perote, 6500 ft, 23 Sep 1938, *Balls 5519* (NY); Peñas-Largas, cerca de Tezoantla, Municipio de Real de Monte, 2750 m, 21 Apr 1966, *Rzedowski 22171* (DS, F, LL). **Puebla:** pine-oak woodland, 74 kms S of the Puebla-Orizaba Rd. (Mex. 150) on road to Nicolas Bravo, 2560 m, 15 Apr 1985, *Grimes 2809* (CAS, MO, NY, TEX); bosque de piño y encino, ca. 1 km al NE de Honey, sobre la terraceria a Pahuatlán, 2050 m, 13 May 1978, *Perino 3336* (CAS, F, MO, WIS); wet ledges of river bluffs below Trinidad Iron Works, 5700 ft, 25 Apr 1904, *Pringle 8911* (A, CAS, CU, F, GH, LL, MIN, MO, MSC, NY, PH, US). **México:** barranca, Distr. Temascaltepec, 18 Feb 1935, *Hinton et al. 7389* (DS, F, LL, MO, NY, US). **Jalisco:** along logging road from El Chante to El Guisar in the Sierra de Manantlán, 2160 m, 17 Aug 1980, *Breedlove & Almeda 45724* (CAS, NY); trail from Real Alto to San Sebastián, 2000 m, 3 Feb 1927, *Mexia 1630* (A, CAS, DS, F, GH, MICH, MIN, MO, NY). **Guerrero:** Vertiente SW del Cerro Teotepec, ca. 17°29'N, 100°12'W, 2900 m, 29 Jan 1965, *Rzedowski & McVaugh 231* (CAS, MICH, MSC). **Oaxaca:** near Tres Cruces S of San José El Pacifico, 10 Feb 1945, *Alexander 665* (MICH, NY); top of the mountain, Zepoaltepetl, 19–27 Feb 1937, *Camp 2649* (DUKE, NY, US); Distrito de Ixtlán; Municipio de Comaltepec, 0.5 km from Hwy. 175 on road to Cerro Humo Chico, 3000 m, 23 Feb 1981, *Martin 341* (CAS, MSC, MO); Cerro Pelón, Municipio de Comaltepec, 2950 m, *Rzedowski 28855* (CAS, MICH, TEX, US). **Chiapas:**

steep slope, evergreen cloud forest on the N and W slope of Cerro Mozotal below the microwave tower along the road from Huixtla to El Porvenir and Siltepec, 30 Dec 1972, *Breedlove & Thorne 31182* (DS, LL, MO, RSA); Mount Hueitepec, 3 mi NW of San Cristóbal de las Casas, 7100–7500 ft, 25 Mar 1949, *Carlson 1582* (F, MICH, NY); Mt. Tacana, 2000–4038 m, Aug 1938, *Matuda 2363* (A, F, MICH, NY, US). **GUATEMALA. Chimaltenango:** north side of Volcán de Fuego, ca. 3600 m, 6 Aug 1960, *Beaman 4024* (GH, MSC); Volcán Acatenango, crater, 13,240 ft, 7 Feb 1907, *Kellerman s.n.* (US); Buena Vista above Tecpán, 10,000 ft, 25 Mar 1933, *Skutch 339* (A, US). **Huehuetenango:** Sierra de los Cuchumatanes, between Chemal and San Juan Ixoy and kms 324 and 325 on Ruta National 9 N, ca. 3140 m, 4 Aug 1959, *Beaman 3053* (DUKE, GH, MSC, NY, TEX, US). **Quetzaltenango:** uppermost ridge of summit of Volcán Zunil, 3000–3800 m, 22 Jan 1940, *Steyermark 34861* (F). **San Marcos:** trail from San Sebastián to Tajamulco volcano, cloud forest near summit, 14 Aug 1979, *Boeke & Utzschneider 2900* (NY); Cerro El Bonete, S of Volcán Tajumulco, 11 Mar 1971, *Plowman 3055* (GH, TEX). **Sololá:** mountain slopes above Santa María, 10,500 ft, 14 April 1937, *Muenscher 12363* (CU, F). **Totonicapán:** ca. 21 km E of Totonicapán at km 153 on Ruta Nacional 1, ca. 3260 m, 8 Aug 1959, *Beaman 3123* (GH, MSC, TEX, US); in moist bank of María Tecun, 3000–3600 m, 12–23 Jan 1966, *Molina R. et al. 16380a* (F, NY, US); summits of Sierra María Tecum between Los Encuentros and Totonicapán, 3200 m, *Williams 14269* (F, GH, MO, US). **HONDURAS. Lempira:** Montaña de Celaque, 2650 m, 18–22 Nov 1974, *Hazlett 2266* (MO). **Ocotepequez:** Cerro El Capitán, 10 km E of Belén Gualcho, 2–15 Apr 1977, *Nelson et al. 4016* (MO). **Olancho:** alrededor de la Picucha, 13 km NE de Catacamas en el Parque Nacional de Agalta, 2 June 1992, *Mejiá Darío 149* (DUKE).

15. Vaccinium wilburii Almeda & Breedlove, Brittonia 44:50. 1992. Type: MEXICO. Guerrero: ridge with *Pinus*, *Quercus*, *Clethra* and *Cleyera*, W of Puerto El Gallo along road to Toro Muerto, 2530 m, 9 Oct 1986 (fl), *Breedlove & Almeda 65040* (holotype: CAS!; isotypes: DUKE! MEXU, MICH, MO! photo NY neg. 13045, NY!).

Epiphytic, erect to pendent *shrubs* with branches 1–2 m long, arising from swollen lignotubers up to 2 dm in diam.; upper branchlets ridged and grooved and there densely spreading puberulent, lower ones becoming terete and glabrate. *Leaves* densely arranged with most internodes ca. 4–7 mm long, the blades persistent, coriaceous, evergreen, lanceolate to lance-elliptic, mostly 2–3.4 cm long, (5–)7–14 mm broad, apically acute the tip itself often blunt, basally broadly cuneate to obtuse, marginally indistinctly and bluntly crenate-serrate, with a narrow, thickened and elevated border, the venation pinnate, with all veins conspicuously elevated on both the upper and lower surfaces at least when dried; petioles subterete, flattened to canaliculate above, 2–4 mm long, puberulent to glabrate. *Inflorescences* axillary, loosely racemose, sometimes corymbose, 5–10-flowered; rachises sharply angled, 1.5–2.5 cm long, glabrous or nearly so; floral bracts narrowly lanceolate to linear, scarious, 2–3 mm long, marginally ciliate; pedicels sharply angled, ca. (8–)12–14 mm long, ca. 0.5 mm in diam., glabrous or nearly so; bracteoles submedial, narrowly lanceolate to linear, scarious, 1.5–2.2 mm long, distally ciliate. *Flowers* 5-merous; calyx ca. 5 mm long, articulate with pedicel, glabrous, the tube ca. 1.5–2.5 mm long, ca. 2 mm in diam., the lobes narrowly triangular to deltoid, acute, ca. 2–2.5 mm long; corolla with aestivation imbricate, membranous, unistratose, cylindric-urceolate, angulate, 7.6–10 mm long, ca. 4 mm in diam., pink, glabrous externally, the lobes ± oblong, obtuse 1–1.5 mm long; stamens 10, included, ca. 6 mm long, the filaments 2.5–3 mm long, flattened, attached medially to anthers, glabrous to ciliolate, the anthers ca. 4–4.2 mm long, lacking spurs, the thecae ca. 1.5–2.3 mm long, slightly papillose, the tubules slender, distinct, ca. 1.6–2.2 mm long and 0.1–0.2 mm in diam., dehiscing by introrse, oblique, terminal pores; styles ca. 11 mm long. Mature *berry* unknown, but at least 5 mm diam. when immature.

Distribution.—Known now only from the montane, pine-oak forests of the Sierra Madre del Sur of the Mexican state of Guerrero, at ca. 2500–3000 m. Flowering and fruiting: Jul, Oct.

Vaccinium wilburii is characterized by its lanceolate to lance-elliptic leaves, glabrous calyx with comparatively long lobes, and uniformly pink cylindric-urceolate corollas that are angulate and glabrous throughout. Although we have not studied this species in the field, the suggestions of Almeda and Breedlove (1992), who stated that the relationships of this species seem to lie with *V.selerianum* (*V. haematinum* to them) and to a lesser extent with *V. lundellianum*, are herein followed.

Additional collections examined: **MEXICO. Guerrero:** Distr. Galeana, Piedra Ancha, oak and pine forest, 3000 m, 29 Jul 1939, *Hinton et al. 14508* (NY, US); Sierra Sur, Mpio. Metlatónoc, Xatu Yahta, al W de Coicoyán (Oaxaca), terrenos de Atzompa, 17°15'N, 98°20'W, 2600 m, 20 Aug 1989, *A. de Avila 737* (CAS).

16. Vaccinium jefense Luteyn & Wilbur, Brittonia 29:272. 1977. *Symphysia jefensis* (Luteyn & Wlbur) vander Kloet, Taxon 53:97. 2004. Type: PANAMA. PANAMÁ: at the top of Cerro Jefé, 1000 m, 5 Jun 1973 (fl), *Luteyn & Kennedy 3955* (holotype: DUKE!; isotypes: MO! NY!).

Lianoid epiphytes or arching terrestrial *shrubs* to 2 m tall; branchlets subterete, glabrous, green becoming reddish-brown, drying brown, the bark thin, cracking into longitudinal strips; twigs subterete, glabrous to densely hirsute distally. *Leaf-blades* persistent, coriaceous, evergreen, elliptic or ovate-elliptic, (4.5–)8–12(–20) cm long, (2–)3–7(–8.5) cm broad, apically acuminate to short-acuminate, basally rounded and cordate to subcordate, marginally entire, dark green above and paler beneath, drying olive to grayish-brown, glabrous above, sparsely to moderately hirsute beneath along the principal veins, the lower surface also with numerous, minute, glandular fimbriae, the venation 5–7(–9)-plinerved or sometimes appearing weakly pinnate with 3 pairs of lateral nerves, the veins impressed above and raised beneath (i.e., the leaves somewhat bullate), proximal 1–2 cm of midrib conspicuously thickened above; petioles terete, rugose, 5–9 mm long, 2–3.5 mm in diam., hirsute to glabrate. *Inflorescences* axillary (rarely appearing terminal), racemose or subcorymbose, (6–)8–17-flowered; rachises subterete, 1–1.5 cm long, glabrous or sparsely hirsute, densely glandular-fimbriate; floral bracts linear-lanceolate, conspicuously nerved, (2.5–)3–9 mm long, ca. 1 mm broad, hirsute, glandular-fimbriate; pedicels terete, striate, ca. (6–)14–26 mm long, 1 mm in diam., sparsely hirsute, densely glandular-fimbriate; bracteoles linear-lanceolate, (2.5–)5–8 mm long, ca. 0.5 mm wide, hirsute, glandular-fimbriate. *Flowers* 5-merous; calyx 6–10 mm long, articulate with pedicel, sparsely to moderately hirsute and glandular-fimbriate, the tube cylindric, conspicuously bluntly and roundedly 10-ribbed or fluted, slightly angled opposite the sinuses, 2–4 mm long, 2–5 mm in diam., the limb campanulate, 4–6 mm long, the lobes oblong to ovate, acute, often basally slightly imbricate, (2–)4.5–6 mm long, 1.7–3 mm broad, conspicuously nerved; corolla with aestivation valvate, thinly fleshy, weakly bistratose, cylindric, 10–13.5 mm long, 5.5–10 mm in diam., green, sparsely hirsute and glandular-fimbriate especially on the surface of the lobes, the lobes triangular, 2–4 mm long and broad; stamens 10, included, ca. 8–10 mm long, the filaments distinct, ca. 2.5–4 mm long, broadest basally, marginally densely sericeous especially on the connective, translucent when fresh, the anthers ca. 7–8 mm long, lacking spurs, orangish-brown when fresh, the thecae ca. 3–3.7 mm long, strongly incurved at the base, papillose, the tubules ca. 3.5–5 mm long, sparsely pilose along inner surfaces, dehiscing by latrorse clefts ca. 1.5–2 mm long; styles included, 9–10 mm long, glabrous. *Berry* spherical, ca. 12 mm in diam., purple, 5-locular.

Distribution.—Elfin forests, densely moss-draped thickets of shrubs and small trees on mountain summits and upper slopes, in Panama from Chiriquí thru Panamá provinces, at 750–1400 m. Flowering: Jan–Jul and sporadically through the rest of the year; fruiting: throughout most of the year.

Vaccinium jefense is characterized by its weakly bullate leaf blades that are basally rounded and subcordate to cordate, conspicuous leaf nervation, glandular-fimbriate (sometimes densely) inflorescences, long and narrow bracteoles, elongate and conspicuously striate calyx limb and lobes, sparsely hirsute corollas (especially on the lobes), and anther tubules that are sparsely long-pilose along the inner surfaces and dehisce by latrorse clefts. It resembles several other green-flowered species of *Vaccinium* and its morphological relationships are mentioned below in the discussion of *V. furfuraceum*.

Additional collections examined: **PANAMA. Chiriquí:** Fortuna, camino de quebrada Bonita, hacia el este del Río Chiriquí, 1150 m, 7 Apr 1987, *Valdespino et al. 560* (NY). **Veraguas:** ridge of Cordillera de Tute, along trail to Cerro Tute, 3–4 km past Escuela Agrícola Alto de Piedra, just W of Santa Fé, premontane and montane rainforest, 8°32'N, 81°07'W, 800–1400 m, 20 Mar 1982, *Knapp & Kress 4367* (MO). **Coclé:** near sawmill above El Copé, ca. 3000 ft, 4 Apr 1978, *Hammel 2363* (MO). **Panamá:** 1 mi después de La Eneida cerca de Cerro Jefé, ± 750 m, 8 Aug 1968, *Correa & Dressler 955* (DUKE, MO, PMA); La Eneida, region of Cerro Jefé, 12 Jul 1968, *Dressler 3541* (DUKE, MO, PMA); path beyond the village of La Eneida, ca. 1000 m, 2 Jul 1970, *Lutyen & Foster 1124* (DUKE, F, MO, US); top of Cerro Jefé, 9 Jul 1966, *Tyson et al. 4344* (DUKE, MO, SCZ).

17. Vaccinium furfuraceum Wilbur & Luteyn, Sida 21:1609, fig. 2. 2005. TYPE: COSTA RICA. LIMÓN: Cantón de Talamanca, fila de exploración minera entre Río Sukut y Río Carbri, Muragubishi, 9°22'50"N, 82°56'50"W, 700 m, 14 July 1989 (fl), *G. Herrera 3286* (HOLOTYPE: INB!; ISOTYPES: DUKE! F! NY).

Much-branched, epiphytic, lianoid *shrubs;* branchlets ± terete, finely ridged and grooved, densely spreading hirsutulous, 1.5–4 mm in diam. *Leaf-blades* persistent, coriaceous, evergreen, ovate to ovate-elliptic, (2.5–)4–6 cm long, (1.2–)1.8–2.5 cm broad, apically acuminate and ± tapering abruptly to the narrowly rounded tip, basally rounded, marginally entire, glabrous above or nearly so except moderately pilose along

the principal veins, moderately to densely spreading pilose beneath along the principal, secondary and even tertiary veins with hyaline trichomes up to 0.7 mm long and also densely beset especially when young with short, thick, glandular, scale-like trichomes ca. 0.1–0.2 mm long on both the veins and the surface, the venation weakly 5-plinerved, the secondary nerves joining together in a series of prominent arches, the lamina ± bullate, the midrib and secondary veins impressed above and elevated beneath and the tertiary veins slightly elevated on both surfaces; petioles 2–3(–4) mm long, densely spreading pilose. *Inflorescences* axillary, congregated distally, sometimes appearing terminal, racemose but with the rachis often contracted and the flowers hence appearing somewhat corymbose, 3–10(–12)-flowered, 2.5–5 cm long overall; rachises (2–)4–8 mm long, densely glandularly strigillose with thickened trichomes 0.1–0.3 mm long and sparingly to moderately pilosulose with hyaline spreading trichomes 0.3–0.6 mm long; floral bracts narrowly lanceolate to linear-lanceolate, 2.5–2.6 mm long, marginally glandular ciliate; pedicels (0.6–)1–2(–2.4) cm long, moderately to densely glandularly strigillose and also sparingly pilosulose with hyaline trichomes; bracteoles located in about proximal third, appressed, linear-lanceolate, glandular ciliate, ca. 2.8 mm long. *Flowers* 5-merous; calyx 3–4.5 mm long, strongly articulate with pedicel, the tube shallowly obconic, ca. 1.5 mm long, ca. 5–6 mm in diam. distally, pronouncedly flaring from the approximately 3 mm in diam. basal portion, densely and scurfily glandular-squamate throughout, the limb ca. 3 mm long, the lobes deltoidly triangular to broadly oblongish with an abrupt distal tip, ca. 1–1.2 mm long, ca. 2.3 mm broad at base; corolla with aestivation valvate, thinly fleshy when fresh but membranous when dry, bistratose, broadly cylindrical, relatively thin in texture, 8–12 mm long, ca. 8 mm in diam. distally, densely scurfily glandular-squamate externally, glabrous internally, the lobes triangular, acute, 2.5–3 mm long, ca. 3 mm broad basally; stamens 10, included, ca. 7–9.5 mm long, the filaments 2–3 mm long, conspicuously hyaline ciliate, flattened, the anthers ca. 7 mm long, lacking spurs, the thecae 2–2.2 mm long, basally incurved, papillose, the tubules ca. 3–5 mm long, dehiscing by latrorse, elongate clefts ca. 1–2 mm long; styles about as long as the corolla, straight, glabrous. *Berry* not seen.

Distribution.—Known only from the type collection made in Costa Rica in the Talamanca foothills of Limón Province, at ca. 700 m. Flowering: Jul.

Vaccinium furfuraceum is characterized by its generally densely glandular-fimbriate leaf blades and floral parts, thin-petiolate leaves with blades that are bullate, apically short-acuminate, and basally rounded, plinerved venation with the reticulate veinlets conspicuously raised beneath, short calyx lobes, thin and membranous corollas that are cylindric-campanulate, and staminal tubules that are pubescent along the inner surfaces and dehiscent latrorsely. The corollas are proportionally conspicuous with respect to the calyx. Its morphological relationships lie near *V. monteverdense* and *V. jefense* with which it has in common pilose inner surfaces of the staminal tubules and latrorse dehiscence. It also shares densely fimbriate leaves and inflorescence parts with *V. jefense*, perhaps its closest relative. *Vaccinium furfuraceum* differs most conspicuously from *V. jefense* by its possession of an overall shorter calyx (3–4.5 mm long vs. 6–10 mm) and calyx lobes (1–1.2 mm long vs. 4.5–6 mm), inconspicuously apophysate (not 10-ribbed) calyx tube, and non-striate calyx limb and lobes.

18. Vaccinium luteynii Wilbur, Sida 21:1612, fig. 3. 2005. Type: PANAMA. Bocas del Toro: Fortuna Dam-Chiriquí Grande Road, 2–3 km N of the Continental Divide, ca. 8°48"N, 82°12'W, 700–760 m, disturbed, steep roadside slopes, 15 Oct 1998 (fl), *Luteyn et al. 15322* (holotype: PMA!; isotypes: AAU, CAS, DUKE, E, G, MO, NY, SCZ, TEX, US).

Terrestrial or epiphytic *shrubs* to 4 m tall; branchlets terete, tan to dull reddish-brown, glabrous. *Leaves* subopposite, the blades persistent, coriaceous, evergreen, ovate to oblong-ovate or ovate-elliptic, ca. 5–15 cm long, 3–6 cm broad, apically acute to somewhat acuminate, basally rounded to almost subclasping, marginally entire and slightly thickened and revolute, glabrous or very nearly so on both surfaces, the venation 3–5 (7)-plinerved with lateral nerves arising from proximal 1/4–1/3 of midrib, midrib proximally much thickened and weakly elevated in basal ¼ above, then thinner and weakly impressed becoming flush to slightly elevated near apex, lateral nerves weakly impressed to flush proximally above but soon slightly elevated distally, reticulate veinlets elevated above, all venation somewhat elevated beneath throughout;

petioles stout, 1–5 mm long, glabrous. *Inflorescences* axillary (often appearing terminal), corymbose racemes, mostly 5–8 cm long overall, 10–13-flowered, with a glabrous to very sparingly and minutely puberulent peduncles; rachises 1.5–4.5 cm long; floral bracts persistent, triangular or lanceolate, scale-like, 2–2.5 mm long, glabrous but often marginally, minutely ciliate; pedicels irregularly angulate or ridged, 20–40 mm long, ca. 0.6–1 mm in diam., glabrous; bracteoles at or very near the base, persistent, subopposite, lanceolate to narrowly triangular, 1.2–2 mm long, glabrous or minutely ciliate. *Flowers* 5-merous; calyx 4–4.2 mm long, articulate with pedicel, the tube subcylindric, deeply and bluntly rugose, ca. 1 mm long, 4–4.5 mm in diam., glabrous, the limb smooth above but broadly and saccately spurred opposite and below each lobe, ca. 3 mm long, the spurs solid (not hollow) and sometimes slightly and broadly bilobed, the lobes triangular, acute, 0.6–1 mm long, glabrous; corolla with aestivation valvate, thick and somewhat fleshy, bistratose, broadly urceolate to urceolate-campanulate, ca. 10 mm long, ca. 8 mm broadest diam. when fresh, but drying 5–8 mm long and ca. 6 mm in diam. just beneath the throat and 3.5–4 mm in diam. just above the calyx, green, externally glabrous and internally densely pilose with sordid, white trichomes especially in the throat and lobes, the lobes acute, ca. 3 mm long; stamens 10, included, ca. 6.5 mm long, the filaments 3.5–4 mm long, long-pilose in distal half, attached to the anther dorsally slightly above its middle, the anthers ca. 3.5 mm long, lacking spurs, golden, the thecae ca. 2–2.5 mm long, densely and finely papillose, the lower third strongly incurved, the tubules ca. 1 mm long, dehiscing by introrse, strikingly oblique pores. *Berry* not seen.

Distribution.—Montane rainforests in Panama, along the continental divide, between Bocas del Toro and Chiriquí, at 700–950 m. All specimens yet seen were collected in flower in Mar.

Vaccinium luteynii is characterized by its subopposite leaves, glabrous leaf blades with rounded to almost subclasping bases, saccately 5-spurred calyx limb, thick, fleshy, broadly urceolate to urceolate-campanulate corollas that are internally densely pilose at the throat and onto the lobes, and glabrous stamens that dehisce introrsely. The interspecific relationships of *V. luteynii* are uncertain at this time, although it is morphologically similar to *V. bocatorense* and *V. floccosum*.

Additional collections examined: **PANAMA. Bocas del Toro:** along road between Florida and Chiriquí Grande, 1.2 mi N of Continental Divide, 5.3 mi N of bridge over Fortuna Dam, 8°44'N, 82°17'W, 910 m, 12 Mar 1985, *Croat & Grayum 60459* (DUKE, MO, NY, PMA, WIS); forest along the Gualaca-Chiriquí Grande road, 31.7 km S of Chiriquí Grande and 15.7 km N of Sitio de Presa, ca. 8°49'N, 82°12'W, 1070 m, *Luteyn 14831* (BRIT, COL, DUKE, MO, NY, P, PMA, SCZ, W); Fortuna Dam-Chiriquí Grande road, 2–3 km N of the Continental Divide, ca. 8°48'N, 82°12'W, 700–760 m, 15 Oct 1998 (fl), *Luteyn et al. 15325* (DUKE, MO, NY, PMA, U), *15323* (BM, CAS, DUKE, MEXU, NY, PMA). **Chiriquí:** Fortuna Dam area, Km. 63 N of dam along road to Chiriquí Grande, ca. 8°48'N, 82°12'W, 890 m, 16 Jan 2003 (bud), *Luteyn & Pedraza 15545* (NY, PMA); Campamento de Bijao-Fortuna, 19 Mar 1976, *Mendoza et al. 260* (DUKE); road from Fortuna Lake to Chiriquí Grande, 5 km along track just S of continental divide wet forest, 8°49'N, 82°12'W, 700 m, *Hampshire & Whiteford 441* (NY, PMA).

19. Vaccinium bocatorense Wilbur, Sida 11:441. 1986 [as *bocatorensis*]. Type: PANAMA. Bocas del Toro: headwaters of Río Colubre, 2400–2550 m (Colubre Camp), 3 Mar 1984, *Gómez et al. 22368* (holotype: DUKE!; isotype: MO! photo NY neg. 13046).

Epiphytic, scandent *treelets* (fide label); branchlets ± terete, drying brownish. *Leaves* apparently subopposite, the blades persistent, coriaceous, evergreen, ovate to ovate-elliptic, 4–6.5 cm long, 3.5–5 cm broad, apically ± rounded, basally rounded and slightly cordate, marginally entire, glabrous above and moderately but inconspicuously erect-pilosulose beneath with widely spaced, slender, hyaline trichomes 0.2–0.3 mm long, apparently eglandular, the venation 5(–7) plinerved with 2–3 pairs of lateral veins arising within 5–10 mm of the base, the midrib and lateral nerves impressed above and elevated beneath, the reticulate venation not apparent; petioles 2–3 mm long, short-puberulent adaxially, ± glabrous abaxially. *Inflorescences* axillary, congregated distally, sometimes appearing terminal, racemose to subcorymbose, 6–12-flowered, 3–7 cm long overall; rachises ± terete, 2–5 cm long, moderately and inconspicuously pilosulose; floral bracts lanceolate to lance-ovate, acute to acuminate, 3–6 mm long, sparingly puberulent to pilosulose externally; pedicels terete, 10–15(–20) mm long, ca. 1 mm in diam., densely but inconspicuously puberulent with erect hyaline trichomes, striate, eglandular; bracteoles borne along the proximal third of the pedicel, lanceolate to lance-oblong, 4–6 mm long, 0.6–1.5(–1.8) mm broad, adaxially glabrous and abaxially sparingly puberulent to pilosulose and marginally ciliate. *Flowers* 5-merous; calyx 7–10 mm long, ca. 6 mm in diam., articulate

with pedicel, inconspicuously and moderately pilosulose with erect trichomes, the tube broadly cylindric, 3.5–4 mm long, pilosulose and glandular-pustulate throughout, the lobes spreading-recurved or reflexed, narrowly triangular to lanceolate, 4–5 mm long, ca. 2–3 mm broad at base; corolla with aestivation valvate, thick and fleshy, bistratose, urceolate to cylindric-urceolate, constricted at throat, 7–9 mm long, 6–7 mm in diam., externally glabrous, internally glabrous or very nearly so for the basal half and increasingly tangled pilose distally, the lobes broadly deltoid, ca. 2–2.5 mm long, 2.5 mm broad at base, exceedingly densely matted tomentose within; stamens 10, included, ca. 5–6.2 mm long, the filaments very weakly connate basally, ca. 2.5–3 mm long and medially ca. 0.5 mm wide, very much flattened and rather broad, marginally and on both surfaces moderately to densely sericeous especially on the connective abaxially, the anthers ca. 3–4 mm long, lacking spurs, golden, the thecae ca. 2.5 mm long, finely or moderately papillose, strongly incurved basally, the tubules 1–1.5 mm long, about as wide as the thecae, glabrous, dehiscing by introrse, oblique pores; styles included, ca. 7 mm long glabrous. *Berry* not seen.

Distribution.—Known only from the type collection, made along the heavily forested headwaters of the Río Colubre, in the province of Bocas del Toro, Panama, at 2400–2550 m. Flowering: Mar.

Vaccinium bocatorense is characterized by its subopposite leaves with stout, rugose petioles, bullate leaf blades with the apices rounded and the bases rounded to subcordate and often somewhat clasping, plinerved venation with the reticulate veinlets obscure beneath, elongate calyx with proportionately long lobes, thick and fleshy corolla that is urceolate to cylindric-urceolate and conspicuously constricted at the throat, and by stamens with introrse dehiscence and glabrous tubules. The corolla is proportionally small and inconspicuous with respect to the calyx. *Vaccinium bocatorense* keys closest to *V. floccosum* and *V. monteverdense* because of their long calyces and calyx lobes, but its overall relationships within the genus are uncertain.

20. Vaccinium floccosum (L.O. Williams) Wilbur & Luteyn, Brittonia 29:272. 1977. *Hornemannia floccosa* L.O. Williams, Brittonia 18:248. 1966. *Symphysia floccosa* (L.O. Williams) L.O. Williams, Phytologia 24:158. 1972. Type: PANAMA. CHIRIQUÍ: Boquete Distr., Bajo Chorro, rainforest, 6000 ft, 11 Jan 1938, *Davidson 104* (holotype: F! photo F neg. 52534; isotypes: A! MO! US!).

Terrestrial or epiphytic *shrubs* 1–4 m tall; branchlets slender grayish to olive-brown, glabrous. *Leaves* alternate to subopposite, the blades persistent, coriaceous, evergreen, ovate to lanceolate or elliptic, (3–)5–9(–11) cm long, (1.5–)3–5(–6.5) cm broad, apically acute to acuminate, basally cuneate to rounded, rarely short-attenuate, marginally entire and slightly thickened, glabrous to moderately appressed glandular-fimbriate above and especially beneath, the venation indistinctly 3–5(–7)-plinerved and also somewhat arcuately veined; petioles 2–4(–6) mm long, glabrous. *Inflorescences* axillary, loose, umbelliform racemes, mostly 2–4 cm long overall; rachises 2–10(–20) mm long, glabrous to sparingly puberulent; floral bracts persistent, ovate to lance-ovate or lanceolate, 1–3.3 mm long, glabrous to sparingly short-ciliate; pedicels 10–20(–25) mm long, glabrous to sparsely puberulous, but distally often fringed with glandular trichomes 0.1–0.2 mm long; bracteoles approximately medial, subopposite, ovate to lance-ovate, persistent, 1–3.2 mm long, glabrous to inconspicuously ciliate. *Flowers* 5-merous; calyx 4–7.8 mm long, articulate with pedicel, glabrous, the tube campanulate, 2–3 mm long, 3–5 mm in diam., the limb longer than the tube, commonly striate, the lobes broadly triangular, acute, 1.8–3.5 mm long; corolla with aestivation valvate, fleshy, bistratose, broadly cylindric-campanulate, broadest at mouth, 7–10 mm long, 4–5 mm in diam., pale greenish often suffused with red, externally glabrous to moderately appressed spiculate, internally densely floccose with a tangle of white, villous trichomes, the lobes erect to spreading or reflexed, triangular, acute, 2–2.2 mm long, densely villous-floccose within; stamens 10, included, ca. 5.2 mm long, the filaments slightly adherent to the very base of the corolla tube, ca. 3–3.2 mm long, flattened, slightly ciliate, the anthers 3–3.5 mm long, lacking spurs, golden, attached along the lower 1/3, the thecae ca. 2.2–2.5 mm long, papillose, basally incurved and bluntly tapering, the tubules inconspicuous, stout, ca. 1–1.2 mm long, dehiscing by terminal, truncate pores. *Berry* spherical, 8–10 mm in diam., dark purplish at maturity, 5-locular.

Distribution.—Elfin and premontane cloud forests in the high land along the border of the Panamanian Bocas del Toro and Chiriquí provinces, between 1000–2500 m. Flowering: Jan–Oct; fruiting: May–Dec.

Vaccinium floccosum is characterized by its alternate to pseudo-opposite leaves with flat blades, entire margins and plinerved venation, conspicuously striate calyx limbs that are longer than the tubes, greenish corollas that are internally densely floccose apically, and anther tubules that are short, ca. 1 mm long, glabrous, and dehiscene introrsely or by perfectly terminal pores. Leaf morphology is variable with populations from the Boquete region showing leaves coriaceous and inconspicuously petiolate, with blades ovate to ovate-lanceolate, with apices acuminate, and bases rounded or short-attenuate. Populations from the Fortuna Dam area show leaves more thinly coriaceous and more conspicuously petiolate, with blades more lance-elliptic, with apices longer acuminate, and bases tapering and cuneate. All leaf blades with rounded bases are also pseudo-opposite, whereas leaf blades with cuneate leaf bases may be either distinctly alternate or pseudo-opposite. The synonymy of this species as listed above indicates something of the extent of its anomalous characteristics. The relationships of this species are as close to the species centered about *Vaccinium poasanum* as they are to the largely West Indian species usually treated as *Symphysia racemosa* (Vahl) Stearn (= *Hornemannia racemosa* Vahl). The inclusion of all these species within *Vaccinium* does not significantly expand the limits of that extremely diverse genus and still seems to us to be the best treatment for the complex until a worldwide revision of the generic limits is undertaken. Vander Kloet (1985), whose study was largely based upon the West Indian *V. racemosum* (Vahl) Wilbur & Luteyn [= *Hornemannia racemosa* Vahl and *Symphysia racemosa* (Vahl) Stern], argued against such an extension of the generic limits of *Vaccinium* claiming that such an expansion "is tantamount to making the genus a dumping ground for any Vaccinieae of uncertain affinity." In Vander Kloet's experience "the character unique to the genus "Vaccinium" is the absence of calyx tube enlargement prior to anthesis" (see vander Kloet 1985 and vander Kloet et al. 2004 for an alternative opinion).

Additional collections examined: **PANAMA. Bocas del Toro:** along trail on divide separating Chiriquí and Bocas del Toro, ca. 8°45'N, 82°15'W, 22 Oct 1985, *McPherson 7232* (DUKE, MO, NY, TEX). **Chiriquí:** trail to Cerro Pate Macho, headwaters of the Río Palo Alto, above Palo Alto, 8°47'N, 82°22'W, 1700–2100 m, 24 Apr 1982, *Knapp & Schmalzel 4784* (DUKE, MO); Boquete Distr., Bajo Mono and Bajo Chorro trails out of Boquete, 1 Jun 1972, *Luteyn 3069* (DUKE, MO, NY); premontane cloud forest along ridge E of Cerro Horqueta, 1700–1900 m, 4 Jan 1975, *Luteyn & Wilbur 4600* (DUKE, MO, NY); slopes approaching Cerro Horqueta, ca. 6.6 km NNE of Boquete, 1500–1800 m, 5 Jan 1975, *Wilbur & Luteyn 19330* (DUKE, F, GH, LL, MICH, MO, NY, PMA, US).

21. Vaccinium monteverdense Wilbur & Luteyn, Brittonia 53:442. 2001. TYPE: COSTA RICA. GUANACASTE: Monteverde area, Hacienda Ira Rosa, 3.7 km above Santa Elena and ca. 1 km before Río Negro just before the Sky Walk, ca. 1500 m, 10 Mar 1999 (fl), *Luteyn et al. 15408* (HOLOTYPE: NY!; ISOTYPE: CR!).

Epiphytic or terrestrial *shrubs*, 1–2 m tall, arising from lignotubers; branchlets ± terete, reddish-brown, glabrous, those of the preceeding year's growth grayish with the bark exfoliating and splitting longitudinally. *Leaf-blades* persistent, coriaceous, evergreen, ovate-lanceolate to elliptic, (2.4–)3.4–8 cm long, (0.8–)1.2–2(–2.7) cm broad, apically somewhat abruptly acuminate to short-acuminate, the tip itself ± bluntly obtuse and ca. 2 mm wide, basally rounded to obtuse, usually short-acuminate and narrowly decurrent onto petioles, marginally entire and revolute causing leaves to be concave, weakly bullate, glabrous on both surfaces, the venation 3(–5)-plinerved with usually only midrib prominent; petioles somewhat angulate and strongly canaliculate, 4–8 mm long, ca. 1.5 mm in diam., glabrous or very nearly so. *Inflorescences* terminal, racemose, 7–9(–16)-flowered; rachises ± terete ca. 2–3(–4.7) cm long, glabrous, reddish; floral bracts inconspicuous, appressed, scale-like, ovate, ca. 0.8–1.5 mm long; pedicels terete, 14–19 mm long, ca. 1–1.2 mm in diam., glabrous, dull reddish; bracteoles nearly basal, subopposite, scale-like, appressed, elliptic to narrowly triangular, ca. 0.6–0.8 mm long. *Flowers* 5-merous; calyx 10–16 mm long, articulate with pedicel, glabrous, green flushed with red, the tube cylindric to obconic, 4.5–8.5 mm long, 2–3 mm in diam. basally and 4–6 mm in diam. proximally and ca. 1 cm in diam. distally, striate to slightly ribbed when dry, the limb spreading to campanulate, 5.5–7.5 mm long, conspicuously striate, the lobes deltoid, 2.5–3.5 mm long, 4–5 mm broad basally; corolla with aestivation valvate, thinly fleshy, bistratose, broadly cylindrical to campanulate, 13–18 mm long, 9–15 mm in diam. distally, green suffused with maroon to reddish-maroon or purplish, glabrous, the lobes ca. 3–3.5 mm long, 3–4 mm broad at base; stamens 10, included, ca. 11.5–12 mm long, the filaments distinct, ca. 4.7–5 mm long, flattened, marginally long-pilose, the anthers ca. 8–8.4 mm long,

lacking spurs, golden, the thecae ca. 3.2–3.4 mm long, papillose, bluntly apiculate basally, the tubules ca. 4.8–5 mm long, distinct, long-pilose along inner surfaces, dehiscing by short, slightly latrorse clefts ca. 1.4–1.5 mm long; styles slender, 12–15 mm long, glabrous. Mature *berry* unknown, but at least 8 mm in diam. and spherical when immature.

Distribution.—Known only from a few collections in cloud forest, from the Costa Rican Cordillera de Tilarán in the vicinity of Monteverde, where the provinces of Alajuela, Guanacaste, and Puntarenas join one another, and also from the Province of Guanacaste in the Cordillera de Guanacaste on the lower slopes of Cerro La Gigante, at ca. 1400–1600 m. Flowering: Jan–Mar.

Vaccinium monteverdense is characterized by having leaf blades with two circular, concave, blackish glands ca. 0.2 mm diam., one on either side of midrib on lower surface, conspicuously striate calyx limb, cylindric-campanulate corolla that is mostly green but suffused with maroon or reddish-maroon apically, stamens that are adherent to the base of the corolla, relatively long filaments, and anthers with pilose tubules that dehisce latrorsely. Furthermore, its leaves are often slightly bullate and concave. The relationships of *V. monteverdense* are uncertain at this time.

Additional collections examined: **COSTA RICA. Guanacaste-Puntarenas-Alajuela:** Cordillera de Tilarán; Monteverde, ca. 1 m S of the Cloud Forest Reserve Field Station, ca. 1460 m, 23 Feb 1986, *Almeda et al. 5082* (CAS). **Guanacaste:** Cordillera de Guanacaste, lower slopes of Cerro La Giganta ca. 2 km W of Río Naranjo, 2600 ft, 27 Feb 1975, *Utley 1885* (DUKE, NY). **Puntarenas:** cloud forest above the Quaker settlement at Monteverde, 1600–1700 m, 4 May 1975, *Utley 2376* (DUKE).

22. Vaccinium campanense Wilbur & Luteyn, sp. nov. (**Fig. 2**). Type: PANAMA. Panamá: Dist. de Capira, Cerro Campana, trocha desde el mirador a la cima, 800 m, 8°41'N, 79°55'W, bosque nebuloso, *Galdames et al. 1840* (holotype: PMA!; isotypes: CAS!, DUKE!, MO!, NY!, SCZ!, US!).

Frutex epiphyticus. Petioli 3–4 mm longi, pilosuli et puberuli. Folia coriacea, integra, ovata vel ovato-elliptica, 2–4.7 × 1.2–2.4 cm, 3–5 plinervia, venatio reticulata, brochidroma. Inflorescentia umbellate-racemosa, 1–2.5 cm longa; rhachis 4–8 mm longa, glandulo-strigillosa et pilosula; pediceli 7–15 mm longi; bracteae caducae. Calyx pedicellis articulatus; tubo cylindrico, 2–3.5 mm longo et 2–3 mm diam., striato, lobato, glandulato; lobi calycis 5, detoidi, 4–5 × 2–2.7 mm, acuti; corolla campanulata, verde, ca. 7–15 × 9–10 mm, lobi corollae triangulari, acuti, ca. 3 × 3.5 mm, stamina 10, thecae granulosae, ± 3–3.6 mm longae.

Epiphytic *shrubs* to 2 m tall; branchlets ± terete, brownish, grayish or blackish, the youngest 1.5–3 mm in diam., finely ridged, inconspicuously puberulous. *Leaf-blades* persistent, coriaceous, evergreen, ovate to ovate-elliptic, 2–4.7 cm long, 1.2–2.4 cm broad, apically usually tapering into a 4–8 mm long, blunt, tongue-like tip, basally usually rounded, marginally entire, the venation 3–5-plinerved, the midrib and secondary veins somewhat sunken above and elevated beneath, the upper surface glabrous at maturity but initially moderately beset with dark reddish, glandular-appressed trichomes that rarely persist into maturity and the sunken veins proximally usually somewhat puberulous, the lower surface moderately beset with minute, often appressed puberulence on the surface and principal veins and those on the surface apparently glandular and darkening reddish-brown upon drying and perhaps 0.1 mm long, usually disappearing with age; petioles terete or nearly so 3–4 mm long, minutely puberulous. *Inflorescences* axillary, racemose, 1–3-flowered, ca. 1–2.5 cm long overall; rachises mostly 4–8 mm long or less, sparingly puberulous to short-pilose; floral bracts 1–1.2 mm long; pedicels 7–15 mm long, sparingly puberulous to short-pilose, drying reddish-brown; bracteoles basal, linear, 1–2(–3) mm long, glandularly minutely ciliate. *Flowers* 5-merous; calyx ca. 8–8.5 mm long, clearly articulate with pedicel, the tube cylindric, 5(–10)-ribbed when fresh, 2–3.5 mm long, 2–3 mm in diam., striate, moderately minutely glandularly appressed pubescent, the limb ca. 5.5 mm long, the lobes triangular, strikingly acute, 4–5 mm long, 2–2.7 mm broad, striate, green, minutely reddish-glandular puberulent; sinuses acute; corolla with aestivation valvate, thinly fleshy, bistratose, broadly campanulate, ca. 7–15 mm long, 9–10 mm in diam., green, the lobes triangular, acute, ca. 3 mm long and 3.5 mm broad at base; stamens 10, included, 9.5–9.6 mm long, the filaments distinct, ca. 3–3.6 mm long and 1.5 mm wide at base, slender but broadening basally, marginally long-ciliate, dorsifixed, the anthers ca. 7.5–8 mm long, lacking spurs, orangish-yellow, the thecae 3–3.6 mm long and 1–1.5 mm wide, finely papillose, the tubules somewhat divergent, each ca. 3–4.6 mm long and 0.5 mm wide, dehiscing by latrorse clefts ca. 1.5–2.5 mm long and 0.5 mm wide; styles slightly exserted. Mature *berry* unknown.

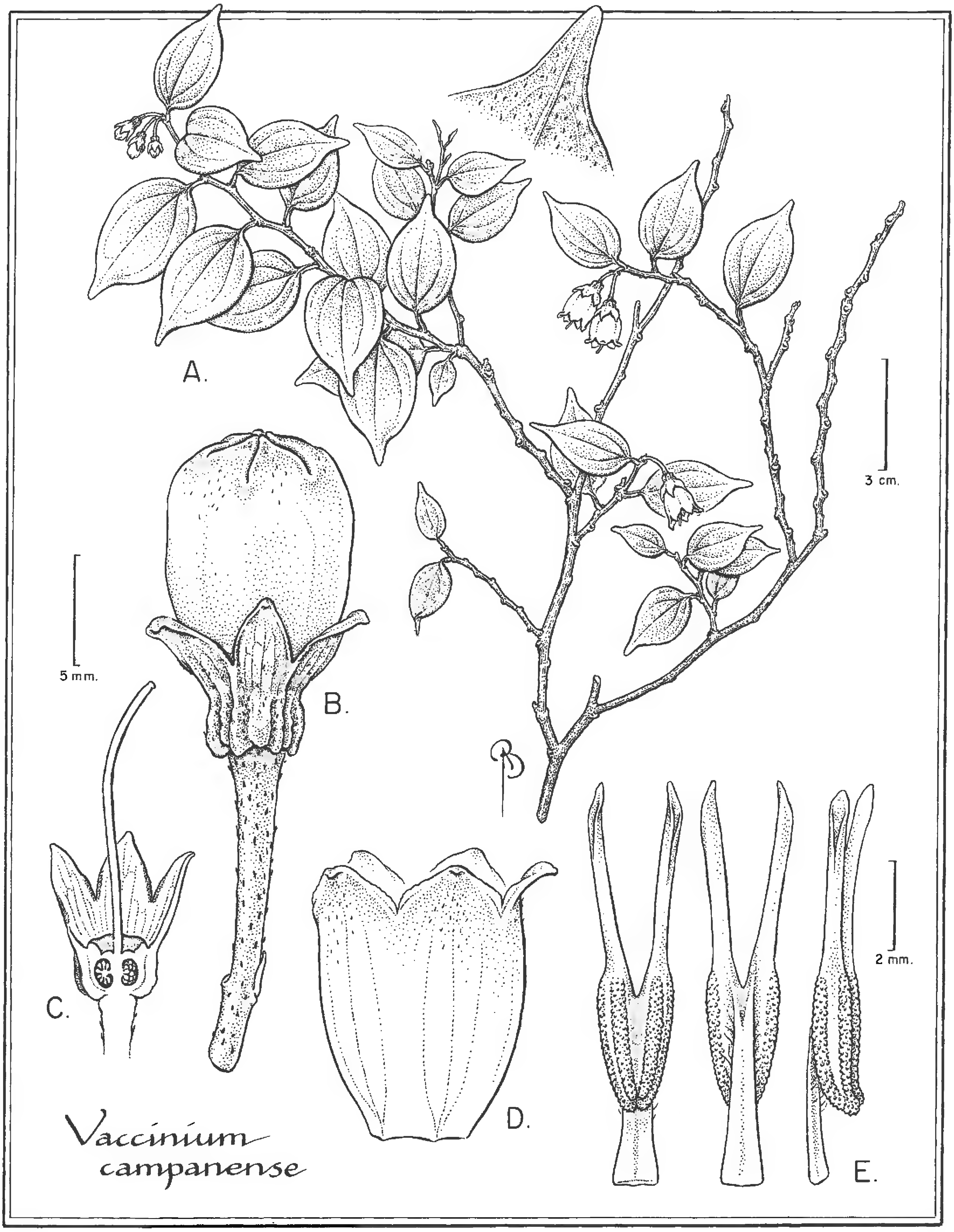

Fig. 2. *Vaccinium campanense* Wilbur & Luteyn. **A,** habit with inset of leaf undersurface showing glandular appressed trichomes and tip. **B,** flower in bud showing valvate aestivation of corolla, calyx tube ribs, and glandular-fimbriate pedicels. **C,** calyx, longitudinal section. **D,** mature corolla. **E,** stamens showing ventral, dorsal, and side views with latrorse dehiscence clefts (drawn from type collection).

Distribution.—Epiphyte in the canopy of cloud forest trees. This very distinctive species has apparently only been collected twice, which is surprising as Cerro Campana is a frequently visited and botanized area relatively close to Panama City, at ca. 800–850 m. Flowering: Feb.

Vaccinium campanense is one of the green-flowered species of *Vaccinium* that is additionally distinguished by its combination of small, entire-margined leaves, few-flowered inflorescences, calyces densely glandular-fimbriate with 5–10 bluntly ribbed tubes and prominently striate, proportionately long and strikingly acute calyx lobes, and broadly campanulate corolla.

Additional collection studied: Cerro Campana, topotype, 13 Feb 1996, *Luteyn & Galdames 14857* (NY) (flowers from forest floor only).

23. Vaccinium poasanum J.D. Smith, Bot. Gaz. (Crawfordsville) 24:395. 1897. *Symphysia poasana* (J.D. Smith) vander Kloet, Taxon 53:97. 2004. LECTOTYPE COSTA RICA. ALAJUELA: Volcán Poas, 2600 m, Mar 1896, *J. Donnell Smith 6634* (LECTOTYPE GH! ISOLECTOTYPE: K! SYNTYPE US! photo NY neg. s.n.).

Terrestrial or epiphytic *shrubs* or small *trees* (1–)2–5(–7) m tall; branchlets glabrous. *Leaf-blades* persistent, coriaceous, evergreen, ovate to lanceolate or elliptic, 3–8(–10) cm long, (1–)2.5–4(–6) cm wide, apically acute to acuminate, basally acute, broadly cuneate or acuminate (very rarely auriculate), marginally entire and slightly revolute, glabrous or sparingly to moderately appressed glandular-fimbriate above and especially beneath, rarely short-puberulent near the base, the venation indistinctly 3–5-plinerved and also somewhat arcuately veined; petioles 1–4 mm long, glabrous to hirsutulous. *Inflorescences* axillary, umbelliform racemes, mostly 2–4 cm long overall, (4–)7–13-flowered; rachises 0.5–2 cm long, glabrous to sparingly puberulent; floral bracts persistent, lance-ovate to lanceolate, 1.5–2.5 mm long, ciliate; pedicels slender, 7–15 mm long, sparingly puberulent, often distally with a fringe of glandular trichomes 0.1–0.2 mm long; bracteoles sub-medial, subopposite, lance-ovate to lanceolate, often persistent, 1–1.5 mm long, ciliate. *Flowers* 5-merous; calyx 3.5–5 mm long, clearly articulate with pedicel, glabrous to densely puberulent, the tube short-campanulate to turbinate, 2–3.5 mm long, about equal in diam., the limb 1–2 mm long, the lobes broadly and shallowly deltoid, apiculate, 0.2–1 mm long; corolla with aestivation valvate, thinly fleshy, bistratose, broadly cylindric, 8–12 mm long, 6–10 mm in diam., pale yellowish or greenish-white and occasionally tinged with bright rose or pink, externally and internally glabrous or rarely apically sparsely villose, the lobes erect to slightly recurved, broadly oblong, apically acute to obtuse, 2–3.5 mm long; stamens 10, included, 7.5–8.5 mm long, the filaments 2–2.5 mm long, ciliate, flattened, broadened basally where slightly adherent to the very base of the corolla, the anthers 6–7 mm long, lacking spurs, golden, attached slightly above the middle, the thecae 1.8–2.2 mm long, papillose, basally incurved, the tubules 3.5–5.5 mm long, glabrous, dehiscing by slightly introrse, oblique pores but appearing ± terminal; styles exserted, 8–10 mm long. *Berry* subspherical, 7–10 mm in diam., dark purple at maturity, 5-locular.

Distribution.—Montane forests and thickets from Guatemala south into central Panama, from 900–3300 m. Flowering: throughout most of year especially from Dec–Mar and Jul–Sep; fruiting: throughout much of the year.

Vaccinium poasanum is characterized by its leaves with acute to broadly cuneate blade bases and acute to acuminate apices, apiculate calyx lobes, broadly cylindric corollas, staminal filaments that are conspicuously shorter than the overall anthers, and elongate anther tubules. Like many other of the green-flowered species of *Vaccinium*, the inter-specific relationships of *V. poasanum* are uncertain. It is, however, morphologically similar to *V. campanense*.

Additional collections examined: **GUATEMALA. Baja Verapaz:** in high forest on hill, Unión Barrios, 13 Mar 1972, *Contreras 11293* (DUKE, LL). **Zacapa:** upper reaches of Río Sitio Nuevo, 1500–1800 m, 25 Jan 1942, *Steyermark 43200* (A, F, NY, US). **HONDURAS. Comayagua:** in cloud forest, 2300 m, Montaña Comayagua, 6 Mar 1975, *Hazlett 2499* (MO). **El Paraiso:** dense cloud forest, Mt. Volcán, 1950 m, 16 Mar 1947, *Williams & Molina R. 12183* (F, GH, US). **Morazán:** along road to Parque Nacional La Tigra, 22–25 km NE of Tegucigalpa; cloud forest, 14°12'N, 87°07'W, 1850–2125 m, 1 Feb 1987, *Croat & Hannon 64045* (DUKE, MO, NY); in rainforest, Mt Uyca, 2000 m, 20 Aug 1964, *Williams & Molina R. 10380* (DS, F, LL, MICH, MO, PH); windswept ridge in cloud forest area, Montaña La Tigra, San Juancito Mts. ca. 15 km NE of Tegucigalpa, 2000–2200 m, *Williams et al. 23273* (CAS, DS, F, LL, MICH, NY, US). **Santa Bárbara:** upper rocky slopes and summit of Cerro Santa Bárbara, 2750 m, 5–6 Apr 1951, *Allen et al 6066* (DS, F, US). **EL SALVADOR.**

Santa Ana: Cerro Montecristo, 6000–6500 ft, 17 Jan 1959, *Allen 7153* (DS, F, LL, NY, US); moist cloud forest, Cordillera Miramundo, Mt. Montecristo, 2000–2200 m, 27–31 Jan 1966, *Molina R. et al. 16711* & *16825* (F, NY, US). **NICARAGUA. Matagalpa:** cut-over cloud forest area, El Porvenir, Cordillera Central, 1700 m, 11 Mar 1967, *Molina R. 20515* (F, NY, US). **Zelaya:** cloud forest and lower elfin forest, Cerro La Pimienta, northern slope facing La Garrapata, ca. 13°45'N, 84°59'W, 900–1180 m, 16 Mar 1980, *Pipoly 6040* (DUKE, MO, NY). **COSTA RICA. Alajuela:** open wooded slopes ca. 1 km from lip of crater and 19 km W of Vara Blanca, Volcán Poas, 2700 m, 21 Jan 1968, *Wilbur & Stone 9843* (DS, DUKE, F, LL, MICH, MO, MSC, NY, US). **Heredia:** Volcán Barba, 8.3 km beyond fork in road at Porrosati, 2600–2800 m, 16 Mar 1975, *Utley 1959* (CR, DUKE, F, MO, NY, US). **Cartago:** SE slope of Volcán Irazú on farm road between CR #8 and Finca Coliblanco, 1–2 km S of Esperanza, 3000–2600 m, 28 Jan 1976, *Utley 3813* (CR, DUKE, F, MICH, MO, NY, US); on lower slopes of Volcán Turrialba, 1–2 km S of Finca Central, 2600–2700 m, 15 Mar 1976, *Utley 4293* (DUKE, MO, NY). **Cartago-San José:** bog and surrounding wooded hills ca. 11 mi SE of El Empalme along Pan American Hwy, ca. 9000 ft, 2 Feb 1970, *Wilbur & Teeri 13901* (DUKE, F). **San José:** Cordillera Central along CR 220 between Alto La Palma and Bajo La Hondura, ca. 4200–3800 ft, 4 Jul 1972, *Luteyn 3315* (DUKE, F, MO, NY); Cerros de Escazu (Cedral), approach to and summit of Cerro Danser ca.. 3–5 km SW of Aserrí, 2300–2400 m, 13 Mar 1976, *Utley 4291* (CR, DUKE, F, MICH, MO, NY, US). **Puntarenas:** Reserva Monteverde, Cerro Negro, 1500–1600 m, *Haber & Bello C. 2814* (DUKE, MO). **Limón:** Cordillera de Talamanca, Atlantic slope, Valle de Silencio along Río Terbi, 0.5–1.5 airline km W of Costa Rican-Panamanian border, 2300–2400 m, 9°08'N, 82°57'W, 9 Sep 1984, *Davidse et al. 28717* (DUKE, MO). **PANAMA. Bocas del Toro:** upper Río Colubre, 2500–3000 m, Aug 1983, *Gómez et al. 21923* (DUKE, MO, NY). **Chiriquí:** mossy forest ca. 7000 ft, E of Guadeloupe along the Río Chiriquí Viejo ca. 2 mi NE of Cerro Punta, ridge of Cerro Respinga, 13 Jan 1971, *Wilbur & Foster 13114* (DAV, DS, DUKE, F, LL, MICH, MO, NY, PMA). **Coclé:** sawmill N of El Cope along divide, 25 Feb 1979, *Hammel 6267* (MO).

24. Vaccinium almedae Wilbur & Luteyn, Sida 21:1607, fig. 1. 2005. Type: PANAMA. Chiriquí: Edwin Fabrega Dam and Reserve in Fortuna, along trail to hydrological station, along Río Hornito, below forestry house along the road in wet forest, 8°45'N, 82°5'W, 1200 m, 20 Jan 1989, *Almeda et al. 6369* (holotype: PMA!; isotypes: CAS! DUKE! NY!).

Coarse, rigid, epiphytic *shrubs* 1–2 m tall; branchlets and branches ± terete, glabrous or nearly so but current season growth not present, thin, brownish or grayish. *Leaf-blades* persistent, coriaceous, evergreen, elliptic, mostly 6–18 cm long, 3–7.5(–9) cm broad, apically acute to acuminate, basally rounded to shortly tapering and sometimes curling or somewhat conduplicate around the petiole at the junction, marginally entire, glabrous on both surfaces, the venation 3–5-plinerved, the veins ± depressed above except the midrib elevated for the proximal third to half while elevated beneath through the 3–4 order and forming an indistinct reticulum; petioles somewhat flattened above and there rather broadly and shallowly canaliculate, mostly 7–15 mm long, 2–3.5 mm in diam., glabrous. *Inflorescenses* mostly ramiflorous, of several to numerous, sessile fascicles (2–10-flowered) emerging from small, depressed mounds 1–2 mm in diam. and 1–2 mm long; floral bracts scale-like, 0.6–1.5 mm long, ciliate; pedicels slender, 5–10 mm long, 0.2–0.3 mm in diam., glabrous; bracteoles deltate, 0.5–0.8 mm long, ciliate. *Flowers* 5-merous; calyx ca. 3–4 mm long, clearly articulate with pedicel, the tube cylindric-obconic, ca. 1.5–2.2 mm long, 1.6–2 mm in diam., glabrous, the lobes broadly based, minute, varying from barely detectable to perhaps as much as 0.2–0.4 mm long, glabrous; corolla with aestivation apparently valvate, membranaceous, thinly bistratose, cylindric to more typically gradually funnelform, 5–9 mm long, flaring to ca. 5–6 mm in diam. from a 2–2.5 mm diam. base, greenish-white, glabrous both externally and internally, the lobes narrowly triangular to deltoid, acute, ca. 2.5 mm long; stamens 10, included, 7–8 mm long, the filaments 1–2.5 mm long, united in the basal 0.5 mm, glabrous, flattened, the anthers 6–7 mm long, lacking spurs, attached medially, the thecae ca. 1.4–2.2 mm long, finely papillose, basally incurved and apiculate, the tubules ca. 3–4.8 mm long, dehiscing by truncate to slightly flaring, terminal pores; styles slightly exserted, glabrous. Mature *berry* unknown, but when immature at least 3–4 mm in diam., glabrous.

Distribution.—Known only from four collections made in wet forest, near the Fabrega Dam site at Fortuna (Chiriquí Prov.) and Cerro Colorado (Bocas del Toro Prov.), Panama, at 1150–1500 m. Flowering: Jan.; immature fruits: Apr.

Vaccinium almedae is characterized by its short-racemose to fasciculate inflorescences that are sometimes ramiflorous, rotate to flaring calyx limb, minute calyx lobes, pale green to white corolla, staminal filaments that are conspicuously shorter than the anthers, and anther tubules that are conspicuously longer than the thecae and that dehisce by truncate to slightly flaring, terminal pores. Its relationships are unclear at this time.

Additional collections examined: **PANAMA. Bocas del Toro:** region of Cerro Colorado 7 mi from Chami Camp, ca. 8°35'N, 81°45'W, ca. 1500 m, 12 Apr 1986, *McPherson 8825* (MO). **Chiriquí:** Fortuna Dam region, along trail to hydrological station on Río Hornito, below forestry house on hwy, 8°45'N, 82°15'W, 1150–1200 m, 20 Jan 1989, *McPherson 13612* (DUKE, MO); Fortuna dam site, along stream on white sandy soil, 1200 m, 7 Feb 1985, *van der Werff & van Hardeveld 6609* (MO, photo NY neg. 13043).

25. Vaccinium santafeense Wilbur & Luteyn, Ann. Miss. Bot. Gard. 65:140. 1978. *Symphysia perardua* vander Kloet, Taxon 53:97. 2004. Type: PANAMA. Veraguas: NW of Santa Fé, 2 km from Escuela Agrícola Alto de Piedra, ridge top cloud forest below summit of Cerro Tute, 27 Mar 1975, *Mori & Kallunki 5248* (holotype: MO!).

Epiphytic *shrubs* 1–2(–3) m tall, vegetatively glabrous throughout; branchlets and twigs terete, gray to light brown when dry. *Leaf -blades* persistent, drying subcoriaceous, evergreen, elliptic, 5–8 cm long, 2–3 cm broad, apically acute to acuminate or even tapering into a pronounced drip-tip 8–12 mm long, basally cuneate, marginally entire, the venation pinnate, the midrib elevated proximally above while sunken distally and beneath elevated throughout; petioles dorsiventrally compressed, 6–11 mm long, 1.5–2 mm broad. *Inflorescences* racemose to subcorymbose, 2–8-flowered; rachises terete, smooth or weakly striate, 5–9 mm long; floral bracts ovate to oblong-ovate, acute, keeled, 1–1.2 mm long, appressed, irregularly and minutely marginally denticulate; pedicels terete, smooth to weakly striate, 8–12 mm long, distally minutely fimbriate; bracteoles basal, slightly smaller and more closely appressed, ca. 1 mm long, minutely denticulate. *Flowers* 5-merous; calyx ca. 3.5 mm long, markedly articulate with pedicel, the tube terete, ca. 2 mm long, 2.5 mm in diam., the lobes broadly triangular with shallowly indented to almost flat sinuses, ca. 0.6 mm long; corolla with aestivation valvate, thin-carnose, bistratose, cylindric, 8–9 mm long, abruptly contracted for the lower 1.5–2 mm and there 2.2–2.5 mm in diam., 4–4.2 mm in diam. above, greenish-white, glabrous both internally and externally, the lobes erect to somewhat recurved, triangular, acute, 2–2.5 mm long; stamens 10, included, 6–7.7 mm long, the filaments distinct, 2–3.2 mm long, ca. 0.5 mm wide, flattened, ciliate, the anthers ca. 5.5 mm long, lacking spurs, the thecae 2–2.5 mm long, finely to coarsely papillose, the tubules 3–3.6 mm long, glabrous, dehiscing by elongate, latrorse clefts 2–3 mm long; styles slightly exserted, 9–10 mm long. Mature *berry* unknown.

Distribution.—Known only from five collections in cloud forest, on or near Cerro Tute ca. 10 km NW of Santa Fé, Veraguas, Panama, at 900–1000 m. Flowering and fruiting: Jan–May.

Additional collections examined: **PANAMA. Veraguas:** NW of Santa Fé, 2 km from Escuela Agrícola Alto Piedra, ridge top cloud forest below summit of Cerro Tute, 27 Mar 1975, *Mori & Kallunki 5249* (MO, photo NY neg. 13044), 28 Mar 1975, *Mori & Kallunki 5280* (MO); Cerro Tute, ca. 10 km NW of Santa Fé, on ridge top in cloud forest, ca. 1000 m, 19 May 1975, *Mori 6254* (MO); along steep trail to summit of Cerro Tute, ca. 3 km above Escuela Agrícola Alto Piedra, near Santa Fé, 2800–3000 ft, 4 Jan 1981, *Sytsma & Antonio 3029* (NY).

26. Vaccinium costaricense Wilbur & Luteyn, Brittonia 29:270, fig. 5. 1977. *Symphysia costaricensis* (Wilbur & Luteyn) vander Kloet, Taxon 53:97. 2004. Type: COSTA RICA. Heredia: vicinity of Cerro Chompipe, 21 Dec 1974, *Wilbur & Luteyn 18579* (holotype: DUKE!; isotypes: CR! F! MO! NY!).

Terrestrial or more typically epiphytic *shrubs*, 1–3(–4) m tall; branchlets grayish to reddish-brown, glabrous. *Leaf-blades* persistent, coriaceous, evergreen, ovate or lanceolate to elliptic, (2.5–)4–8(–11) cm long, (1.5–)2.5–4.5(–6.2) cm broad, apically acute to acuminate, basally acutely tapering to rounded, marginally entire and slightly thickened, appearing slightly revolute, glabrous to moderately but inconspicuously appressed glandular-strigillose both above and more especially beneath, the venation 3–5(–7)-plinerved and also somewhat weakly arcuately veined; petioles 1–2 mm long, glabrous. *Inflorescences* axillary but often superficially appearing terminal, of umbelliform racemes, 10–15-flowered; rachises 1–2.5(–3) cm long, glabrous to very sparingly and minutely puberulent; floral bracts persistent, ovate-lanceolate to lanceolate or triangular, scale-like, 1–3.5 mm long, glabrous to minutely ciliate; pedicels mostly 10–30 mm long, glabrous to inconspicuously puberulous or often indistinctly distally fringed with glandular trichomes ca. 0.1 mm long; bracteoles usually in the lower third, ± subopposite, lance-ovate to lanceolate, persistent, 0.8–3 mm long, appressed, glabrous to indistinctly ciliate. *Flowers* 5-merous; calyx 3.5–5(–5.8) mm long, clearly articulate with pedicel, glabrous to densely, minutely puberulent, the tube campanulate, ca. 2–2.5(–4) mm long, 2.5–3 mm in diam., the lobes triangular, acute, 1.2–1.8(–2) mm long; corolla with aestivation valvate, fleshy,

bistratose, broadly cylindric to somewhat urceolate, 5–8 mm long, 4–7 mm in diam., pale greenish-yellow, externally glabrous and internally moderately to densely pilose with sordid, white trichomes especially in the throat and on the lobes, the lobes erect to spreading or somewhat reflexed, triangular, acute, 1–2 mm long; stamens 10, included, ca. 6 mm long, the filaments 3–4 mm long, flattened, slightly adherent to the very base of the corolla tube, slightly ciliate, the anthers ca. 3–4 mm long, lacking spurs, golden, attached in the lower quarter, the thecae ca. 1.8–2 mm long, papillose, basally incurved and apiculate, the tubules stout, ca. 1–2 mm long, dehiscing by introrse, slightly oblique or slightly flaring, terminal pores. *Berry* spherical, 11–16 mm diam., dark maroon to blackish-maroon, or purple, 5-locular.

Distribution.—Mountain slopes covered by premontane rainforests, on Atlantic slope of Costa Rica (Heredia and San José) and Continental Divide forests in Panama (Bocas del Toro and Chiriquí), between (700–)1100–2000 m. Flowering and fruiting: throughout much of the year.

Vaccinium costaricense is characterized by its combination of acutely tapering to rounded leaf blade bases, a calyx tube that is longer than the limb, corollas that are pilose internally at the throat, and short anther tubules. *Vaccinium costaricense* has a longer rachis, shorter calyx limb and lobes, smooth, not striate, calyx limb and lobes, and longer anther tubules than its morphologically closest relative *V. floccosum*, from western Chiriquí Prov., Panama. These differences in the calyx may be influenced by where and how the plants grow, i.e., epiphytes in the closed forest vs. terrestrial in exposed, windswept areas (JLL, pers. observ.). *Vaccinium costaricense* differs from *V. orosiense* by acutely tapering to rounded leaf blade bases (not cordate and amplexicaul) and shorter calyx lobes (at least in the Costa Rican populations). The characters that distinguish these three species of *Vaccinium* are admittedly few and more collections are needed to help clarify their morphologies and relationships.

Additional collections examined: **COSTA RICA. Heredia:** forest between Río Pejé and Río Sardinalito, Atlantic slope of Volcán Barva, 10°17.5'N, 84°04.5'W, 700–800 m, 3 Apr 1986, *Grayum 6706* (DUKE); primary forest near Río Las Vueltas, NE of Volcán Barba, 1950 m, 25 Jun 1972, *Lent 2645* (DUKE, NY, PMA); forests between Río Las Vueltas and Quebrada Cabrú, vicinity of Cerro Chompipe, 1700–2000 m, 21 Dec 1974, *Luteyn & Wilbur 4438* (DUKE, F, MO, NY); vicinity of Cerro Chompipe between Río Las Vueltas and Río Nuevo, 1800–2000 m, ca. 12 km NNE of San Rafael, 21 Dec 1974, *Wilbur & Luteyn 18576* (DUKE, F, MICH, MO, NY, US). **San José:** CR 216, ca. 3–6 km beyond Las Nubes in vicinity of Cascajal on NW flank of Volcán Irazú, 5700 ft, 10 Dec 1975, *Almeda et al. 2626* (CAS, DUKE); pastured slopes and thicket at Alto La Palma ca. 15 km in straight line NE of San José, 1480 m, 13 Jul 1976, *Wilbur 20339* (CR, DUKE, F, LL, MICH, MO, NY, PMA, US, WIS). **PANAMA. Bocas del Toro:** along road between Fortuna and Chiriquí Grande, 1.2 mi N of Continental Divide, 5.3 mi N of bridge over Fortuna Dam, 8°44'N, 82°17'W, 910 m, 12 Mar 1985, *Croat & Grayum 60459* (DUKE, NY). **Chiriquí:** east of the Fortuna main campsite, 1200–1600 m, 12 Sep 1977, *Folsom & Dressler 5300* (DUKE, MO); windswept ridge 10 km N of Los Planes de Hornito, IRHE Hydroelectric Project, 1150 m, 18 Jun 1982, *Knapp & Vodicka 5603* (DUKE, MO); forested slope along ridge, vicinity of Fortuna Dam, ca. 8°45'N, 82°15'W, ca. 1250 m, 28 Apr 1986, *McPherson 9094* (DUKE, MO, NY).

27. Vaccinium orosiense Wilbur & Luteyn, Brittonia 29:275. 1977. *Symphysia orosiensis* (Wilbur & Luteyn) vander Kloet, Taxon 53:97. 2004. TYPE: COSTA RICA. CARTAGO: steep slopes above the Río Grande de Orosi, on property of ICE Hydroelectric plant ca. 15–20 km upstream from the suspension bridge, 1300–1800 m, 20 Dec 1974, *Luteyn et al. 4411* (HOLOTYPE: DUKE!; ISOTYPES: CR! F! MO! NY! US!).

Epiphytic or terrestrial *shrubs*, 1–2 m tall; branchlets glabrous, olivaceous to purplish. *Leaves appearing subopposite, the blades* persistent, coriaceous, evergreen, ovate to ovate-lanceolate, (2–)4–9(–14) cm long, (1.5–)3–5(–7) cm broad, apically acute, basally rounded to more typically cordate, clasping to amplexicaul, marginally entire and slightly thickened, glabrous to sparsely and inconspicuously appressed, glandular-strigillose, the venation indistinctly 5–7(–9)-plinerved; petioles ca. 1 mm long, glabrous. *Inflorescences* axillary but often superficially appearing terminal, of umbelliform racemes mostly 2–4 cm long overall; rachises mostly 1–1.5 cm long, glabrous; floral bracts persistent, triangular to ovate-lanceolate, scale-like, 1–2.2 mm long, glabrous to minutely ciliate; pedicels mostly 15–25 mm long, glabrous; bracteoles usually in the lower quarter, subopposite, deltoid to lance-ovate, persistent, 0.8–1.5 mm long, appressed, glabrous to inconspicuously ciliate. *Flowers* 5-merous; calyx 2–4 mm long, clearly articulate with pedicel, glabrous, the tube campanulate to urceolate, ca. 2–3 mm long, 2.5–4 mm in diam., the lobes triangular, acute, 0.5–1.2 mm long, glabrous; corolla with aestivation valvate, fleshy, bistratose, cylindric to urceolate, 5–8 mm long, 5–7 mm in diam., yellowish-green often suffused with maroon, externally glabrous and internally moder-

ately to densely pilose with white trichomes especially on the lobes and the upper half of the tube, the lobes spreading or reflexed, triangular, acute, 1–1.2 mm long; stamens 10, included, ca. 6 mm long, the filaments ca. 3 mm long, flattened, weakly adherent to the very base of the corolla tube, villous, the anthers ca. 4 mm long, lacking spurs, golden, attached medially, the thecae ca. 1.5–2.3 mm long, papillose, basally incurved and apiculate, the tubules stout, ca. 1.5–2 mm long and 0.5 mm wide, dehiscing by slightly introrse, oblique pores. *Berry* spherical, ca. 12 mm diam., "morada," 5-locular.

Distribution.—Known only from the heavily forested slopes above the Río Grande de Orosi near Tapantí (Cartago), Costa Rica, and from the Fortuna area, Panama (Chiriquí), at 1130–1800 m. Flowering and fruiting: apparently extends through much of the year.

Vaccinium orosiense is characterized by its amplexicaul leaves with rounded or cordate blade bases, short calyx lobes, corollas that are moderately to densely pilose internally at the throat, and by short anther tubules. When fresh, the basal region of the leaf blades is red, as is also the case in *V. costaricense*, *V. floccosum*, and *V. luteynii*, but usually not in *V. poasanum*. The relationships of *V. orosiense* are mentioned under the discussion of *V. costaricense*.

Additional collections examined: **COSTA RICA. Cartago:** Hwy 224 on property of ICE Hydroelectric Plant, ca. 11.6–20 km E of the church in Orosi, steep roadside banks, 1500–1700 m, 29 Dec 1973, *Almeda et al. 2180* (DUKE, F, GH, MO, NY, US); Tapantí Hydroelectric project, wet road bank, 13 Dec 1975, *Utley 3623* (CR, DUKE, F, MO). **PANAMA. Chiriquí:** Fortuna, camino de quebrada Bonita llegando por el embalse hacia el norte, 1130–1150 m, 8 Apr 1987, *Valdespino et al. 631* (DUKE, NY) [JLL thinks *Valdespino 631* may be *V. luteynii*]; Gualaca-Fortuna Dam site road, 10.1 mi NW of Los Planes de Hornito, 1260 m, 10 Apr 1980 (fl), *Antonio 4194* (MO).

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BOOK REVIEW

Perry K. Peskin. 2006. **The Search for Lost Habitats: 30 Years of Exploring for Rare and Endangered Plants—Book 1.** (ISBN 1-933197-16-1, pbk.). Orange Frazier Press, P.O. Box 214, Wilmington, Ohio 45177, U.S.A. (**Orders:** www.orangefrazer.com, 1-800-852-9332, Customer Service Department, Orange Frazer Press; or The Three-Hour Press Company, 3559 Strathavon Road, Shaker Heights, Ohio 44122, U.S.A.). $34.95, 288 pp., numerous color images and photographs, 8 7/8" × 8".

Want to go exploring in captivating new habitats? Want to set out on a fantastic search for rare and unusual plants? Want to enjoy a great nature walk with a knowledgeable guide? If you answered yes to any of these questions, then you will enjoy the new book by Perry Peskin, *The Search for Lost Habitats: 30 Years of Exploring for Rare and Endangered Plants—Book 1.* Peskin has provided a great outdoor field adventure that you can enjoy without getting muddy or devoured by insects!

Author Peskin has been engaged in exploring the natural world since 1975. *The Search for Lost Habitats* is his first book sharing his curiosity of nature and his intriguing searches for rare and exotic plants in both the Midwest and Canada. The book consists of fifteen standalone essays on various topics. Some of the essays are explorations of specific locations such as the Lynx prairie, the area originally explored by Ohio botanist/naturalist Lucy Braun. There are also chapters that discuss specific habitats such as Ohio's so-called "invisible prairies", while the chapter "Pennsylvanian nature trail" explores the historical geology of an area. A few chapters provide information on oddities such as the parasitic plant dodder or salt-loving halophytic plants. And other chapters are focused on plant families like orchids and the folks who love them or specific rare species of mallows and the search to discover them.

The author has written *The Search for Lost Habitats* to be very accessible to most readers. Some basic botanical knowledge would be helpful, but the book is unassuming and readable by any interested person. The author has provided helpful information within the text of the current Endangered Species Act regarding status of those species discussed. Peskin has also included many colorful photographs of plants integrated into the various essays. Additional photographs of habitats, interesting plants, and animals in various regions of the Midwest and Great Lakes regions are in Appendix A. Appendix B includes common plant names, scientific epithets, and U.S. status under the Endangered Species Act. A bibliography and an index complete the text. Although habitat and specific locations are discussed, the author has wisely altered names and locations so as not to allow potential plant thieves ready access to rarities.

The Search for Lost Habitats is thoroughly enjoyable and a boon to nature lovers. As a former resident of southern Ohio and a graduate of The Ohio State University, this book brought back very fond memories of both childhood hikes and college field trips—one of which was to the Lakeside Daisy State Nature Preserve, where I saw the unique limestone habitat these plants inhabit (Lakeside daisies are discussed in Essay 4). Peskin draws you into his book and gives you enough information using both text and color photos to visualize and experience the location or plant discussed. I look forward to Book Two of the series.—*Lee Luckeydoo, Botanical Research Institute of Texas, 500 East 4th Street, Fort Worth, Texas 76102-4025, U.S.A.*

RE-DISCOVERY AND TYPIFICATION OF *THIBAUDIA LAURIFOLIA*, *MACLEANIA INSIGNIS*, AND *M. COCCINEA* (ERICACEAE: VACCINIEAE), AN ADVENTUROUS HISTORY

James L. Luteyn

Institute of Systematic Botany
The New York Botanical Garden
Bronx, New York 10458-5126, U.S.A.
jluteyn@nybg.org

ABSTRACT

Herbarium work has now revealed the true identity of and the ability to typify *Thibaudia laurifolia* M. Martens & Galeotti, *Macleania insignis* M. Martens & Galeotti, and *Macleania coccinea* Decne. **Orthaea laurifolia** (M. Martens & Galeotti) Luteyn is proposed as a new combination.

RESUMEN

El trabajo de herbario ha revelado la identidad verdadera de las especies y la posibilidad de tipificar *Thibaudia laurifolia* M. Martens & Galeotti, *Macleania insignis* M. Martens & Galeotti y *Macleania coccinea* Decne. Se propone **Orthaea laurifolia** (M. Martens & Galeotti) Luteyn como combinación nueva.

INTRODUCTION

In 1967, Yeo wrote a nice little paper entitled "Notes on some species of *Macleania* (Ericaceae)." That paper helped to sort out the taxonomy and nomenclature for numerous species of *Macleania*, the species numbered 1–15 in Smith's (1932) monograph of the Thibaudieae. That group was characterized by having a single anther tubule and connate staminal filaments, the subgenus *Macleania* as defined by Luteyn (1997), several of which are still cultivated. Yeo recognized Smith's taxonomy as "largely satisfactory, but that he [Smith] has misinterpreted a number of type specimens." On pages 51–56 of the article, Yeo discussed *M. insignis* with its numerous synonyms. Yeo's attempt to clarify the typification of some of these names was also largely satisfactory, but the types of three names discussed below still need further clarification.

Henri Galeotti was one of the first botanical explorers of Mexico. His collections were offered for sale and this explains their dispersion over many institutions. However, the herbarium (BR) of the National Botanic Garden of Belgium acquired large quantities of Galeotti material on two separate occasions. A first and the largest part was purchased after Galeotti's death in 1858, as reported in the minutes of the meeting of 14 February 1859 of the "Société royale d'Horticulture" [which later became the National Botanic Garden]. This was not a complete set, however, of Galeotti's Mexico collection of ca. 7300 specimens (perhaps only about half). Much later, in 1932, Pierre Martens donated the herbarium of his father Martin Martens to BR. It contained circa 2000 Galeotti specimens that M. Martens himself had examined with Galeotti. Upon his return from Mexico, the horticulturist Galeotti developed a collaboration with M. Martens (himself a professor in chemistry and botany at Louvain). The main output was the "*Enumeratio synoptica plantarum phanerogamarum* ...," identifying the Mexico collection and published in a long series of articles presented at the meetings of the "Académie royale des Sciences et Belles-Lettres de Bruxelles" (Martens & Galeotti 1842–1845) (pers. comm. 2008 with E. Robbrecht).

It is with the aforementioned brief introduction that I set the context for the typifications mentioned in this paper.

Thibaudia laurifolia M. Martens & Galeotti

In 1842 (page 530), Martens and Galeotti described *Thibaudia laurifolia* based on *Galeotti 1814* (protologue: leaves short-petiolate, acuminate; racemes elongate, 6–8-flowered). In 1932, in his classic "The American

Species of Thibaudieae," A.C. Smith cited the *Galeotti 1814* sheets at B and US as the "type collection of *Thibaudia laurifolia.*"

Unfortunately, *Galeotti 1814* is now seen to be a mixed collection of at least four elements based on material seen at BR, G, K, NY, P, US, and W. These include examples of *Macleania insignis*, *Satyria warszewiczii* Klotzsch, an unknown species possibly *Satyria panurensis* (Benth. ex Meisn.) Benth. & Hook.f. ex Nied., and the true *Thibaudia laurifolia*. Based on my studies, there were at least 11 herbarium sheets numbered as *Galeotti 1814* including one destroyed at B (after A.C. Smith had seen it), but not including the fragments at F. All the duplicate collections of *Galeotti 1814* seen, except the herein designated lectotype, have original printed Galeotti herbarium labels (Fig. 1A) that cite the collection locality as "Chinantla" and [Oaxaca] "Mexico," and the collector as "H. Galeotti." All the duplicates were identified as *Macleania insignis*, with the exception of the lectotype sheet. They are represented by:

B = *Macleania insignis* (fide A.C. Smith 1932; not seen since destroyed during WWII)

BR (barcode S.P. 627855) = *Thibaudia laurifolia* [bearing modern printed red annotation label "TYPUS," and an original hand-written specimen collection label in the hand of Martin Martens that reads "Thibaudia laurifolia Nobis" (Fig. 1B) [based on figs. 2–3 in Dorr (1986), and pers. comm. 2008 with E. Robbrecht]; =lectotype of *Thibaudia laurifolia* and *Orthaea laurifolia* comb. nov. fide this paper]

BR = *M. insignis* (recently incorrectly annotated as "TYPUS" by means of a red felt-tip pen in an unknown hand; not seen by Smith; photo NY neg. 12557)

BR = *M. insignis* (unannotated, bearing only an original printed Galeotti herbarium label that has on it the hand-written "Thibaudia laurifolia H. Galeotti")

BR = unknown Ericaceae, perhaps *Satyria warszewiczii* (bearing original printed Galeotti herbarium label that has on it the hand-written "Thibaudia laurifolia, nobis")

F = *M. insignis* (fragment ex P correctly annotated as *M. insignis*, no mention of type status)

F = *M. insignis* (fragment ex G incorrectly annotated as isotype of *T. laurifolia*)

G = *M. insignis* (mounted on two sheets, bearing original printed Galeotti herbarium label that has on it the hand-written "Thibaudia," and incorrectly annotated as "type coll. of Thibaudia laurifolia M. & G." by Smith in 1932; photo F neg. 26647)

P = *M. insignis* (incorrectly annotated as "type coll. of Thibaudia laurifolia M. & G." by Smith in 1931, by Sleumer in 1959, and also by Luteyn in 1978)

US (sheet 573239; barcode 00113543) = *M. insignis* (bearing original printed Galeotti herbarium label that has on it the hand-written "Thibaudia" (Fig. 1A), and incorrectly annotated as "type coll. of Thibaudia laurifolia M. & G." by Smith in 1930)

W (sheet no. 117232) = *M. insignis* (bearing original printed Galeotti herbarium label that has on it the hand-written "Thibaudia laurifolia H. Gal." and an annotation label as *Macleania insignis* by Cufondontis in 1933)

W (sheet no. 117231) = unknown Ericaceae, perhaps *Satyria panurensis* (bearing W herbarium label that reads "1814. Thibaudia laurifolia H. Gal." and an annotation label as *Macleania insignis* by Cufondontis in 1933)

LECTOTYPIFICATION OF *THIBAUDIA LAURIFOLIA*

Orthaea laurifolia (M. Martens & Galeotti) Luteyn, comb. nov. Basionym: *Thibaudia laurifolia* M. Martens & Galeotti, Bull. Acad. Roy. Sci. Bruxelles 9(2):530. 1842, non Blume, Bijdr. Fl. Ned. Ind. 859. 1826. Type. MEXICO. Oaxaca: Chinantla, 4000 ft, May (fl), *H. Galeotti 1814* (lectotype, designated here: BR (barcode S.P. 627855), photo NY neg. 12556).

Empedoclesia stipitata Luteyn, Brittonia 28:403, fig. 2. 1976[1977]. *Orthaea stipitata* (Luteyn) Luteyn, Nord. J. Bot. 7:33. 1987. Type. MEXICO. Oaxaca: Comaltepec, Ixtlan, La Esperanza, 1524 m, 19 Apr 1970 (fl), *MacDougall 606.5* (holotype: NY).

The sheets of *Galeotti 1814* from B and US that A.C. Smith (1932) cited as the "type collection of *Thibaudia laurifolia*" in his "The American Species of Thibaudieae" are now both seen to be *M. insignis*. In that same paper, on page 369, Smith also included *Thibaudia laurifolia* in the synonymy of *Macleania insignis*. He did not see (or at least did not annotate) the specimens of either *Galeotti 1814* or *1827* at Brussels (BR), but relied on sheets at B and US for his concept. Thus he did not know that *Galeotti 1814* was a mixed collection; therefore, he synonymized *Thibaudia laurifolia* under *Macleania insignis*. Nevertheless, the only specimen that fits the protologue of *T. laurifolia* is one of the sheets at BR, which Smith did not see, and which bears an original hand-written specimen collection label (Fig. 1B) that perfectly matches the handwriting sample for Martin Martens kept at BR (pers. comm. 2008, E. Robbrecht). That sheet has now been properly annotated as the lectotype of *T. laurifolia* and the remaining sheets as *Macleania insignis*, *Satyria warszewiczii*, or *Satyria* cf. *panurensis*.

In 1976, Luteyn described *Empedoclesia stipitata* based on *MacDougall 606.5* (holotype: NY). Later,

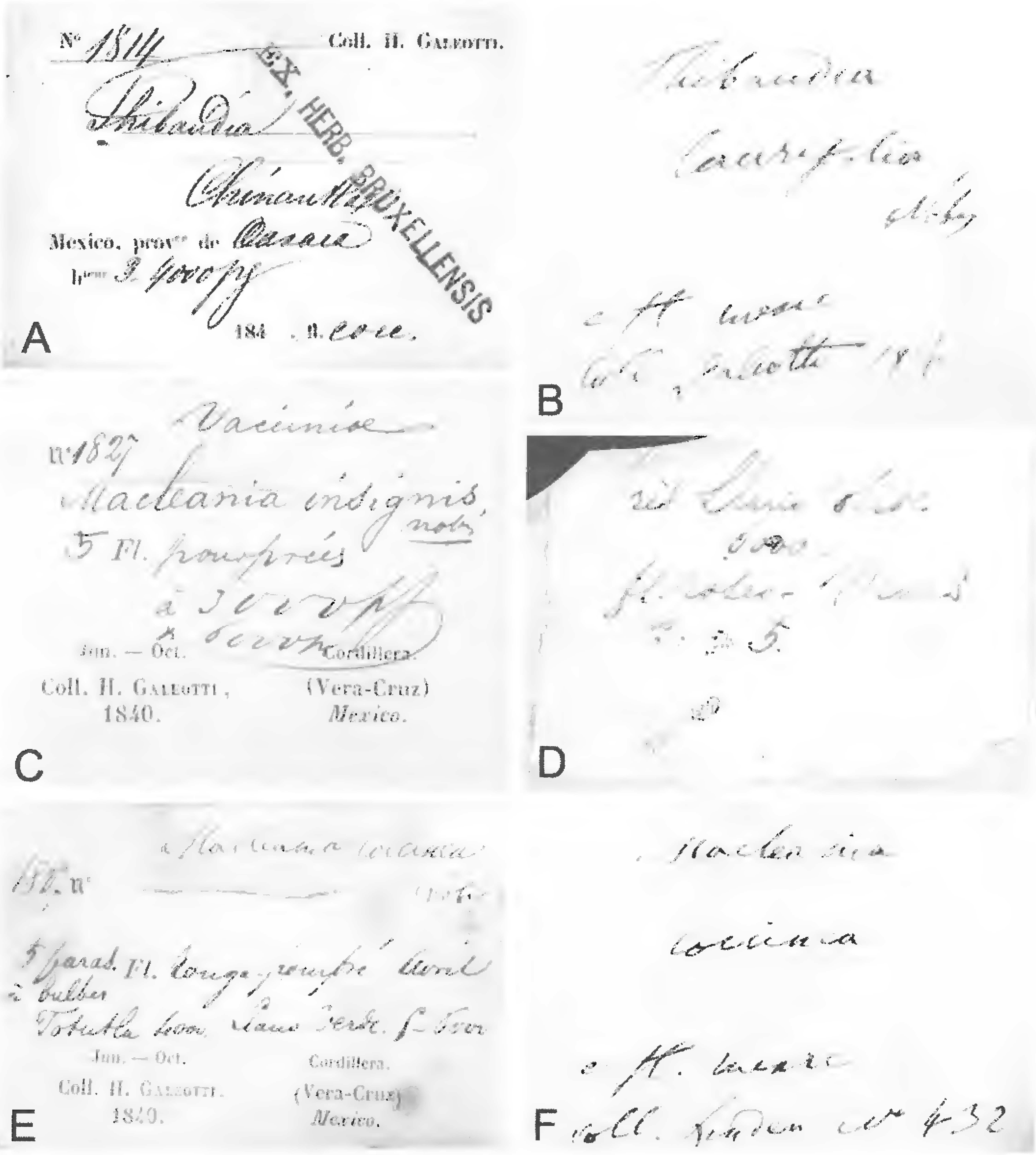

Fig. 1. Herbarium labels showing hand writing of Henri Galeotti and Martin Martens, all probably 1840s. **A,** Original printed Galeotti herbarium label in the hand of Galeotti from US duplicate of *Galeotti 1814* (*Macleania insignis*). **B,** Original hand-written specimen collection label in the hand of M. Martens from BR sheet of *Galeotti 1814*, the lectotype of *Thibaudia laurifolia*. **C,** Original printed Galeotti herbarium label in the hand of H. Galeotti from BR sheet of *Galeotti 1827*, the lectotype of *Macleania insignis*. **D,** Original hand-written specimen collection label in the hand of H. Galeotti also from BR sheet of *Galeotti 1827*, the lectotype of *Macleania insignis*. **E,** Original printed Galeotti herbarium label in the hand of H. Galeotti from BR sheet of *Galeotti 1827*, a syntype of *Macleania insignis* as well as the lectotype of *Macleania coccinea*. **F,** Original hand-written specimen collection label in the hand of M. Martens from BR sheet of *Linden 432*. [E. Robbrecht (BR) kindly identified handwriting based on samples kept at BR]

Luteyn (1987) synonymized the genus *Empedoclesia* Sleumer under the genus *Orthaea* Klotzsch and made the new combination *Orthaea stipitata* (Luteyn) Luteyn. As a result of herbarium studies carried out in the United States (F, GH, MO, NY, US) and in Europe in 1986, 2006, and 2007 (B, BR, CGE, E, G, K, L, MA, OXF, P, S, W), it is now clear that both *Thibaudia laurifolia* and *Orthaea stipitata* represent the same species. Therefore, the new name becomes *Orthaea laurifolia* (M. Martens & Galeotti) Luteyn.

Macleania insignis

Martens and Galeotti (1842, page 531) also described *Macleania insignis* in the same article as above, based on *Galeotti 1827* (protologue: leaves subsessile, ovate, obtuse, 3-nerved; flowers fasciculate). The protologue stated that the species was found on oaks near to the German colony of Mirador at 4000 feet elevation, and that it was also found in the eastern cordillera of Oaxaca near Talea and Llano-Verde at 5000 and 6500 feet.

Based on my studies, there were at least nine herbarium sheets numbered as *Galeotti 1827* including one destroyed at B, but not including the fragments at F. The original printed Galeotti herbarium labels of all the duplicates of *Galeotti 1827* (Fig. 1C,E) give the general locality as "Cordillera, (Vera Cruz) Mexico," along with the dates of "Jun.–Oct." and "Coll. H. Galeotti, 1840," although the individual labels of some of the duplicates seen at BR(2x), G, K(2x), NY, and P have three small differences with regards to more specific hand-written information. Two of the sheets at BR mention Llano Verde at 6000 feet (Fig. 1D), while the sheets at G and P give no specific locality, but do say the plants were "parasite" on oaks; the K-Herb. Hook. sheet says "parasite on oaks at 4–6000 ft." One of the BR sheets that was relatively recently designated as "HOLOTYPUS" by P. Bamps (curator at BR) bears two hand-written labels at the bottom of the sheet—one an original hand-written specimen collection label mentioning "Prés Llano Verde 6000" (Fig. 1D), and the other an original printed Galeotti herbarium label that reads "Macleania insignis, nobis" (Fig. 1C). This is the only sheet upon which the original printed Galeotti herbarium label gives the word "nobis". The two labels match the handwriting of H. Galeotti based on personal communication in 2008 with E. Robbrecht (BR). This I feel means that this sheet was seen by the authors and is appropriate to designate as the lectotype, which is how I have annotated it. The W sheet reads "Macleania insignis nobis," but does not have an original printed Galeotti herbarium label nor is it written in a recognized hand. The other *Galeotti 1827* sheets have all been annotated by me as syntypes. All of these are identified as *Macleania insignis* and are represented by:

B = *Macleania insignis* fide A.C. Smith 1932 (not seen since destroyed during WWII)

BR (barcode S.P. 627888) = *M. insignis* [lectotype, annotated as "HOLOTYPUS" by P. Bamps, bearing also an original printed Galeotti herbarium label that reads "Macleania insignis, nobis" (Fig. 1C), and a second hand-written specimen label that reads "Près Llano Verde 6000" (Fig. 1D), both in the hand of H. Galeotti (pers. comm. 2008 with E. Robbrecht)]

BR (barcode S.P. 627921) = *M. insignis* (syntype, without recent annotation, but bearing original printed Galeotti herbarium label with hand-written "Macleania coccinea Nobis" in the hand of H. Galeotti (Fig. 1E); photo NY neg. 12555; also herein designated as neotype of *M. coccinea*).

F = *M. insignis* (syntype fragment ex G; voucher for F neg. 26646)

G = *M. insignis* (syntype, correctly annotated "TYPE COLL." by Smith in 1932; photo F neg. 26646)

K-Herb. Benth. = *M. insignis* (syntype, correctly annotated as "TYPE COLL." by Smith in 1931)

K-Herb. Hook. = *M. insignis* (syntype, correctly annotated as "TYPE COLL." by Smith in 1931)

NY = *M. insignis* (syntype, duplicate ex W)

P = *M. insignis* (syntype, correctly annotated as "TYPE COLL." by Smith in 1931, by Sleumer in 1959, and also by Luteyn in 1978)

W (sheet no. 0008497) = *M. insignis* (syntype, with unrecognized hand-written label reading "Macleania insignis nobis")

TYPIFICATION OF *MACLEANIA INSIGNIS*

Macleania insignis M. Martens & Galeotti, Bull. Acad. Roy. Sci. Bruxelles 9(2):531. 1842. Type. MEXICO. Vera Cruz: Cordillera, Llano Verde, 6000 ft, Jun–Oct, 1840, *Galeotti 1827pp* [lectotype, here designated: BR (barcode S.P. 627888), photo NY neg. 12554].

Macleania coccinea

The name "Macleania coccinea" was first introduced in the protologue of *M. cordata* Lem. (Lemaire 1848). In that publication, which included a color illustration of the new *M. cordata*, Lemaire mentioned that his new

species was cultivated at the establishment of "M. Jacob-Makoy, de Liége," having been introduced alive in 1842 or 1843 by "M. Ghiesbregt" along with two other species "les *M. coccinea* ... et *insignis*...."

In 1851, Decaisne formally described *Macleania coccinea* from a cultivated plant collected by A.B. Ghiesbrecht, presumably from Mexico (see Yeo 1976). The protologue (Decaisne 1851) included a description of the new species (in French), a paragraph about cultivation techniques for species of *Macleania,* and a beautiful color illustration of *M. coccinea* that as Yeo (1976) mentioned is "very similar" to the one of *M. cordata*. It does not, however, give any information about the original collection or its locality; therefore, the actual location of any type material is still uncertain. There are two herbarium specimens at BR bearing the name *M. coccinea*, the one of *Linden 432* (barcode S.P. 627954) from the "Collection Martin Martens," donated to BR by Pierre Martens in 1932, bears the name "Macleania coccinea" on an original hand-written specimen collection label in the hand of Martin Martens (pers. comm. 2008, E. Robbrecht) (Fig. 1F). The second sheet, *Galeotti 1827pp* (type number for *M. insignis*), also ex "Collection Martin Martens," donated to BR by Pierre Martens in 1932, has the more explicitly written name "Macleania coccinea Nobis" in the hand of Galeotti on an original printed Galeotti herbarium label that gives the general locality as "Cordillera, (Vera Cruz) Mexico," along with the dates of "Jun.–Oct." and "Coll. H. Galeotti, 1840" (Fig. 1E). These are the only two herbarium sheets that I have seen that bear the name *M. coccinea*. Since Decaisne's types are supposedly at BR (Stafleu & Cowan 1976, page 607), I am herewith designating the latter sheet as the neotype of *Macleania coccinea*, the collection number of which is itself a syntype of *M. insignis*.

TYPIFICATION OF *MACLEANIA COCCINEA*

Macleania coccinea Decne., Rev. Hort. [Paris], sér. 3, 5:301, t. 16. 1851. Type. MEXICO. Vera Cruz: Cordillera, "Totutla, 4000 [ft], Llano Verde 4–6000 [ft]," Jun–Oct, 1840, *Galeotti 1827pp* [neotype, designated here: BR (barcode S.P. 627921), photo NY neg. 12555].

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REVISION OF *SIPHONANDRA* (ERICACEAE: VACCINIEAE), A GENUS ENDEMIC TO PERU AND BOLIVIA

James L. Luteyn

Institute of Systematic Botany
The New York Botanical Garden
Bronx, New York 10458-5126, U.S.A.

Edgardo M. Ortiz

Herbarium Areqvipense (HUSA)
Universidad Nacional de San Agustín de Arequipa
PERU

ABSTRACT

The genus *Siphonandra* is revised. Two new species, **Siphonandra nervosa** Luteyn & E.M. Ortiz and **Siphonandra santa-barbarense** Luteyn & E.M. Ortiz, are described, illustrated, mapped, and put into the context of a key to the five known species in the genus. An additional two species, *Siphonandra elliptica* and *Siphonandra magnifica*, are lectotypified.

RESUMEN

Se revisa el género *Siphonandra*. Se describen e ilustran dos nuevas especies, **Siphonandra nervosa** Luteyn & E.M. Ortiz y **Siphonandra santa-barbarense** Luteyn & E.M. Ortiz. Adicionalmente se incluye una clave para las cinco especies del género y se lectotipifican dos especies, *Siphonandra elliptica* y *Siphonandra magnifica*.

INTRODUCTION

Siphonandra is a small, distinctive, high-elevation genus of five species that are endemic to the geographical range from northern Peru (Amazonas) to northern Bolivia (Cochabamba). It was named by Klotzsch (1851) on the basis of its long and slender staminal tubules, but is also characterized by its articulate calyx, usually connate filaments, and perfectly terminal pores at the tips of the tubules (Smith 1932; Luteyn 1998, 2002b). *Siphonandra elliptica*, the type species, spans the entire geographical range of the genus from northern Peru (Amazonas) to northern Bolivia (Cochabamba), where it is common. The other four species, however, are only known from one collection site each, thus making it difficult to assess relationships between any of the species in this genus. The description of *Siphonandra nervosa* and *S. santa-barbarense* brings to three the number of species found in Peru and to five the number described overall in the genus, which until a few years ago was only known from the widespread *S. elliptica* (see Luteyn 2002a).

Smith (1932) compared *Siphonandra* morphologically with *Lysiclesia* (=*Orthaea*), *Ceratostema*, and *Orthaea* on the basis of their having in common the characters of articulate calyces and anther dehiscence through apical pores, although he believed that these similarities were "doubtless derived by distinct and somewhat parallel courses." It is true that the genus *Siphonandra* is morphologically most similar to those species of *Ceratostema* that have anther dehiscence by perfectly terminal pores (but there are about as many species in *Ceratostema* that have dehiscence through oblique or lateral pores); both genera have articulate calyces, large corollas, and equal stamens with very slender anther tubules with apical dehiscence. The major differences are that *Ceratostema* has corolla lobes proportionally very long and narrow (usually greater than 4 mm long) and its corolla is also usually basally ventricose, whereas *Siphonandra* has corolla lobes very short (equal to or less than 2 mm long) and its corolla is cylindric with parallel sides along its entire length. Also the geographical ranges of the two genera do not overlap, with *Ceratostema* ranging from Venezuela to northern Peru (Piura, Cajamarca), north of the Huancabamba Depression, whereas *Siphonandra* ranges from northern Peru (Amazonas), south of the Huancabamba Depression, and into northern Bolivia (south to Cochabamba). *Orthaea* seems more distantly related having alternately unequal stamens.

Morphological and molecular studies clarify that *Siphonandra* is definitely found within the blueberry tribe Vaccinieae (Kron et al. 2002a). The only published molecular phylogeny of Vaccinieae that included *Siphonandra* (Kron et al. 2002b) used *mat*K and ITS data, which placed *Siphonandra* within an "Andean clade" sister to a polytomous group containing *Sphyrospermum*, *Disterigma*, and one species of *Ceratostema*.

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A subsequent study within the "Andean clade" did not include *Siphonandra* (Powell & Kron 2003). Therefore, the overall data that was based on only one sequence from one species of *Siphonandra* seems premature and there is still uncertainty about its affinities.

KEY TO THE SPECIES OF *SIPHONANDRA*

1. Filaments distinct.
   2. Rachis to 0.5 cm long, 3–6-flowered; calyx ca. 9 mm long, the tube densely bearing squamiform, carnose warts; corolla 35–37 mm long ____ **3. Siphonandra magnifica**
   2. Rachis 12–25 mm long, 10–22-flowered; calyx 6–10 mm long, the tube without warts; corolla 18–26 mm long ____ **5. Siphonandra santa-barbarense**
1. Filaments connate.
   3. Corolla 43–48 mm long ____ **1. Siphonandra boliviana**
   3. Corolla ca. 25 mm long.
      4. Leaf blades lanceolate, (3.5–)5.5–8.5 × (1–)1.5–3 cm, apically shortly and bluntly acuminate, marginally entire, the lateral nerves 6–8 per side; inflorescences 3–4-flowered, the rachis to 0.7 cm long; pedicels to 7 mm long ____ **4. Siphonandra nervosa**
      4. Leaves oblong, ovate-oblong, or slightly obovate, 3–5.5 × 1–2.5 cm, apically obtuse or subacute, marginally entire or faintly crenulate, the lateral nerves 3–5 per side; inflorescences 5–15-flowered, the rachis striate, 1.5–5 cm long; pedicels 7–20 mm long ____ **2. Siphonandra elliptica**

TAXONOMY

Siphonandra Klotzsch, Linnaea 24:24. 1851. *Ceratostema* Juss. sect. *Siphonandra* (Klotzsch) Hook. f. ex Benth. & Hook. f., Gen. Pl. 2:570 p.p. 1876. Type species: *Siphonandra elliptica* (Ruiz & Pav. ex G. Don) Klotzsch.

Siphonostema Griseb. in Lechl. Berb. Amer. Austr. 58. 1857, nom. nud. Type species: *Siphonostema myrtifolium* Griseb.

Terrestrial or often epiphytic **shrubs. Leaves** alternate, with blades coriaceous, evergreen, marginally recurved and entire or faintly crenulate; pinnately nerved, short-petiolate; axillary bud scales 2, valvate. **Inflorescences** axillary, solitary, racemose, with 5–22 pedicellate flowers; floral bract inconspicuous; bracteoles 2. **Flowers** (4–)5-merous, without odor; aestivation valvate; calyx articulate with pedicel, the tube short-cylindric, terete to narrowly winged, the limb spreading, the lobes 5; corolla cylindric; **stamens** 10, equal, often slightly longer than corolla, the filaments distinct to connate, equal, shorter than anthers, the anthers basifixed, lacking spurs, lacking disintegration tissue, the thecae granular, the tubules distinct to base, elongate, slender, flexible, about half as wide (or less) as thecae, 4–5 times longer than thecae, dehiscing by strictly terminal, slightly flaring pores; pollen without viscin threads; ovary inferior; style filiform, slightly exserted; nectariferous disc annular. **Fruit** a spherical berry.

The current generic concept follows that of Klotzsch (1851) and Smith (1932), but differs by the acceptance of species with distinct staminal filaments (vs. connate in original concept) as first noted by Sleumer (1941).

1. Siphonandra boliviana Luteyn, Sida 20:13–15. 2002. (**Fig. 1**). Type. BOLIVIA. La Paz: Prov. Bautista Saavedra: Charazani, W of Chullina, 3400 m, 1 Aug 1994 (fl), *B. Herzog H200* (holotype: NY; isotypes: LPB, n.v., LZ, n.v.).

Shrubs (size unknown); mature branches terete, glabrous, the bark exfoliating in thin strips; immature branches subterete, sometimes shallowly angled or ribbed, short-pilose with white hairs; axillary bud scales ca. 2 mm long, short-pilose. **Leaves** with blades coriaceous, elliptic to oblanceolate, 2.5–5.5 × 1–1.8 cm, basally cuneate, apically broadly acute to nearly obtuse, marginally entire, the lamina essentially glabrous above or sparsely short-pilose proximally along midrib, sparsely pilose beneath especially along midrib, also provided with reddish-brown, basally swollen, glandular fimbriae beneath; pinnately nerved with 4–6 secondary veins anastomosing near margin, the midrib and secondary veins impressed above and raised beneath, the reticulate veinlets plane to slightly impressed above but inconspicuously raised beneath; petioles rugose, subterete, broadly flattened above, 4–5 mm long. **Inflorescences** ca. 20-flowered, apparently nodding; rachis subterete, striate to angled, at least 5 cm long (still in bud, apparently still elongating), densely short-pilose with white hairs; floral bract ovate, acuminate, 3–4 mm long, densely short-pilose; pedicels subterete, striate to angled, 11–13 mm long, densely short-pilose as rachis; bracteoles located in proximal

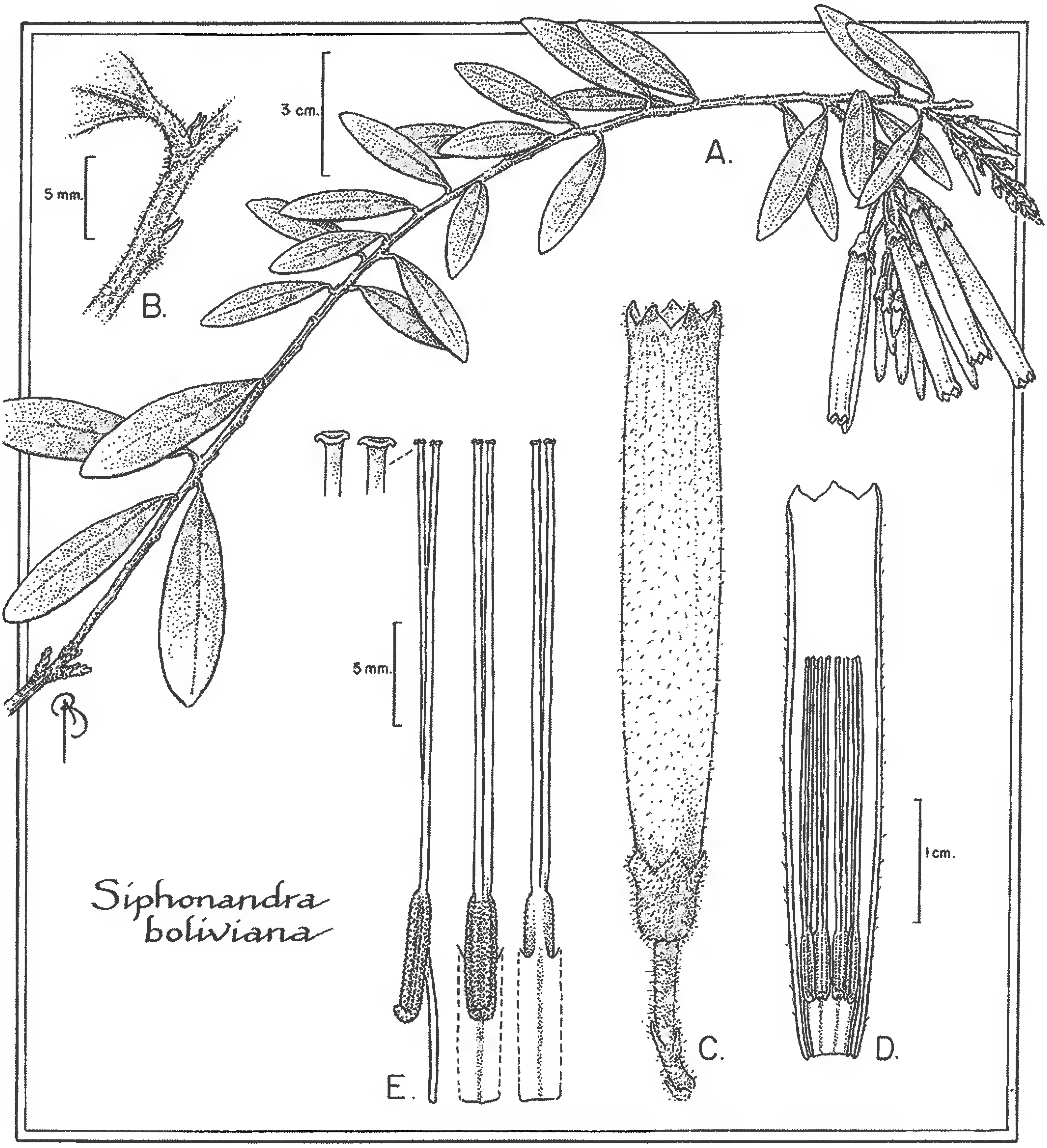

Fig. 1. ***Siphonandra boliviana*** **Luteyn. A. Habit. B. Portion of stem showing pubescence, leaf attachment, and axillary bud scales. C. Flower showing floral bract, pedicel, bracteoles, calyx, and corolla. D. Longitudinal section of corolla showing position of stamens. E. Stamens showing lateral, ventral, and dorsal views with details of terminal dehiscence pores. (Drawn from type collection).**

1/3 pedicel, similar to floral bract, 2–3 mm long. **Flowers** with calyx 7–8 mm long, densely short-pilose as rachis, the tube cylindric, ribbed, 4–5 mm long, rounded at base, the limb spreading-campanulate, 3.8–4.5 mm long, the lobes deltate, acute, 1.5–2 mm long; sinuses obtuse; corolla long-cylindric, 43–48 mm long, 6–7 mm diam., short-pilose throughout with white hairs, the lobes deltate, acute, ca. 2 mm long; **stamens** ca. 32 mm long, the filaments connate, ca. 7 mm long, glabrous, the anthers ca. 28 mm long, the thecae granular, ca. 6 mm long, incurved at base, the tubules ca. 22 mm long; style about equaling corolla. **Berry** not seen.

Icones.—see Luteyn 1998, 2002 (Fig. 1).

Distribution (Fig. 2).—Endemic to Bolivia (La Paz) and known only from the type collection, which was made in a *Weinmannia* forest at 3000–3500 m. Rare and endangered.

Siphonandra boliviana is easily distinguished morphologically from the other two species by the characters mentioned in the key and diagnosis.

2. Siphonandra elliptica (Ruiz & Pav. ex G. Don) Klotzsch, Linnaea 24:24. 1851 (**Fig. 3**). *Thibaudia elliptica* Ruiz & Pav., Fl. Peruv. Chil. 4: pl. 384, fig. b. 1802, nom. nud. *Thibaudia elliptica* Ruiz & Pav. ex G. Don, Gen. Hist. 3: 861. 1834. *Ceratostema ellipticum* (Ruiz & Pav.) Benth. & Hook. f., Gen. Pl. 2: 570. 1876. *Euryganía elliptica* (Ruiz & Pav.) Britton, Bull. Torrey Bot. Club 20:137. 1893. Type. PERU. Muña, Pillao and Acomayo, *Ruiz & Pavón s.n.* [lectotype, here designated by Luteyn: MA! (numbered "15/50" and barcoded MA747445; photo F neg. 29347)]. I suspect that G. Don validated the name in *Thibaudia* based simply on the plant illustrated by Ruiz and Pavón, and not on an actual specimen he saw. Illustrations: Hooker. Icones pl. 2: t. 108. 1837. The Hooker illustration is based on "Cuesta of Huanacabra, Andes of Peru. *Mathews*. (n. 884)" which is at K (1 full sheet and another 1/2 sheet), probably BM, CGE, and OXF also. See also Luteyn 1998. [There is a "884" numbered collection without collector or locality at BM, which also has the hand-written name "Ceratostema corymbosa" written on its label; at OXF too. We do not know of any citation anywhere of the name "C. corymbosa," which must be unpublished.] (Fig. 3).

Siphonostema myrtifolium Grisebach in Lechl., Berb. Amer. Austr. 58. 1857, nom. nud. Type collection cited: *Lechler 2276* (K!). The K sheet is not formally marked as type except by annotation label of ACS in 1931. The sheet at G was annotated as *S. elliptica* by ACS in 1932.

Siphonostema costatum Grisebach in Lechl., Berb. Amer. Austr. 58. 1857, nom. nud. Type collection cited *Lechler 2053* (K!). The K sheet is not formally marked as type except by annotation label of ACS in 1931. The sheet at G was annotated as *S. pilosa* by ACS in 1932.

Ceratostema hookeri Britton, Bull. Torrey Bot. Club 20:137. 1893, nom. illeg. Britton based this new name on the *Thibaudia elliptica* illustration in W.J. Hooker's, Icon. Pl. t. 108 (1837), non Ruiz & Pavón (1802). I think Britton created this unnecessary name when he noted the difference in illustrations between Ruiz and Pavón's plant and that of Hooker (just as I do). Although the descriptions seem to match, the plant illustrated by Ruiz and Pavón (1802) and that of the lectotype itself at MA show leaves that are nearly plinerved with 3–5 nerves per side; whereas, the illustration of Hooker (1837) shows a plant with definitely pinnately nerved leaves. Britton cited *Rusby 2036* (NY) from Mapiri, Bolivia, as an example of his new species.

Ceratostema weberbauerii Hoerold, Bot. Jahrb. Syst. 42: 316. 1909. Type. PERU. Puno: Sandia, 3100–3300 m, Apr 1902 (fl), *Weberbauer 740* (holotype: B, destroyed).

Siphonandra pilosa A. C. Smith, Contrib. U.S. Natl. Herb. 28(2):355. 1932. *Ceratostema pilosum* (A.C. Smith) J. F. Macbride, Univ. Wyoming Publ. 11: 42: 1944. Type. BOLIVIA. La Paz: Larecaja: Cerro de Tuile, vic. Tacacoma, 3350 m, May or June 1860, *Mandon 549* [holotype: NY; isotypes: G(4x; photo F neg. 26655), K-Herb. Hook., P(3x)].

Terrestrial or epiphytic **shrubs** to 2 m tall; mature stems terete, glabrous, the bark cracking in thin, longitudinal strips yellowish to light brown in color; immature stems subterete, striate, puberulous when young, glabrate or persistent; axillary bud scales 2, valvate, ovate, acuminate to apiculate, striate, ca. 3–4 mm long, not pseudo-stipular. **Leaves** with blades thick-coriaceous, oblong, ovate-oblong, or slightly obovate, 3–5.5 × 1–2.5 cm, basally cuneate, apically obtuse or subacute, marginally entire or faintly crenulate, slightly revolute, the lamina glabrous or sparsely brownish-pilose above, pilose to sparsely pilose beneath with scattered, appressed, dark brown hairs ca. 0.4–0.5 mm long, glabrate, often strongly punctuate on both surfaces from deciduous glandular fimbriae; pinnately nerved, the midrib impressed above, prominent beneath, the secondary nerves 3–5 per side, spreading, ascending at margin, slightly impressed above, plane to raised beneath, the reticulate veinlets copious, sometimes obscure, plane; petioles subterete, rugose, 3–5 mm long, puberulous or glabrous. **Inflorescences** 5–15-flowered, deciduously bracteate at base with several, ovate bracts ca. 1.5–2 mm long; rachis striate, 1.5–5 cm long, glabrous or pilose with copious, pale, spreading hairs to 0.3 mm long; floral bract deciduous, ovate, acuminate, ciliate with white hairs to 1 mm long, the lamina glabrous, ca. 3.5–4 mm long; pedicels rugose, 7–20 mm long, pilose or glabrous, bearing several minute, cartilaginous teeth at apex; bracteoles basal, ovate, acuminate, ca. 1.5–3 mm long, ciliate. **Flowers** with calyx ca. 7–8 mm long, the tube cylindric, sometimes 5–10-ribbed, ca. 3–3.5 mm long, glabrous to pilose with short, pale, spreading hairs, the limb 3.5–4.5 mm long, the lobes to ca. 1.5–3 mm long; sinuses broadly rounded; corolla cylindric, 20–26 mm long, 4–5 mm diam., glabrous to sparsely pilose, red with whitish or pale greenish tips when fresh, the lobes triangular, obtuse to subacute, ca. 1–1.5 mm long; **stamens** ca. 25 mm long, the filaments connate (supposedly rarely distinct in type of *S. weberbauerii*), ca. 5–6 mm long,

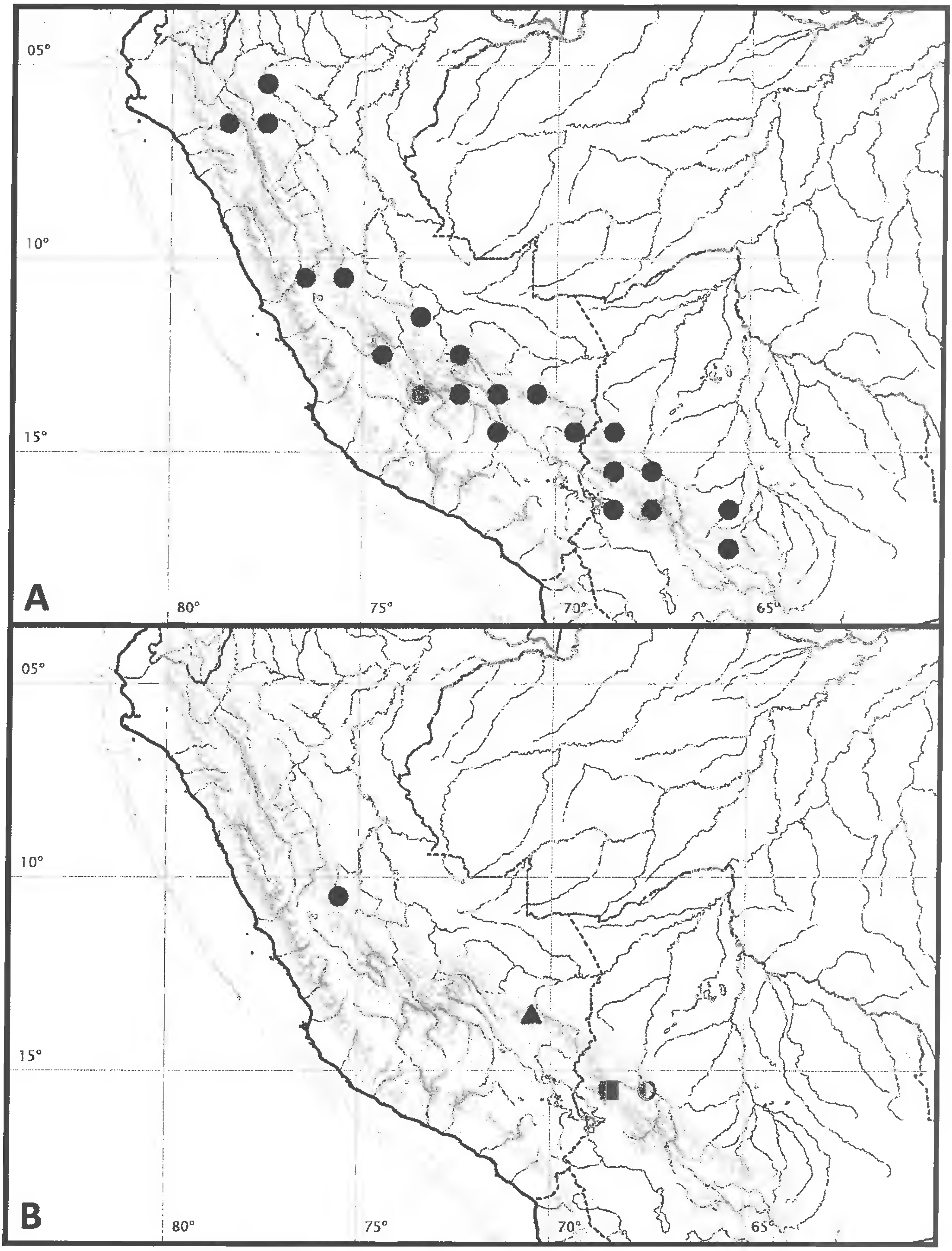

Fig. 2. Distribution of species of *Siphonandra*. A. ● *S. elliptica*. B. ● *S. santa-barbarense*; ▲ *S. nervosa*; ■ *S. boliviana*; ◐ *S. magnifica*.

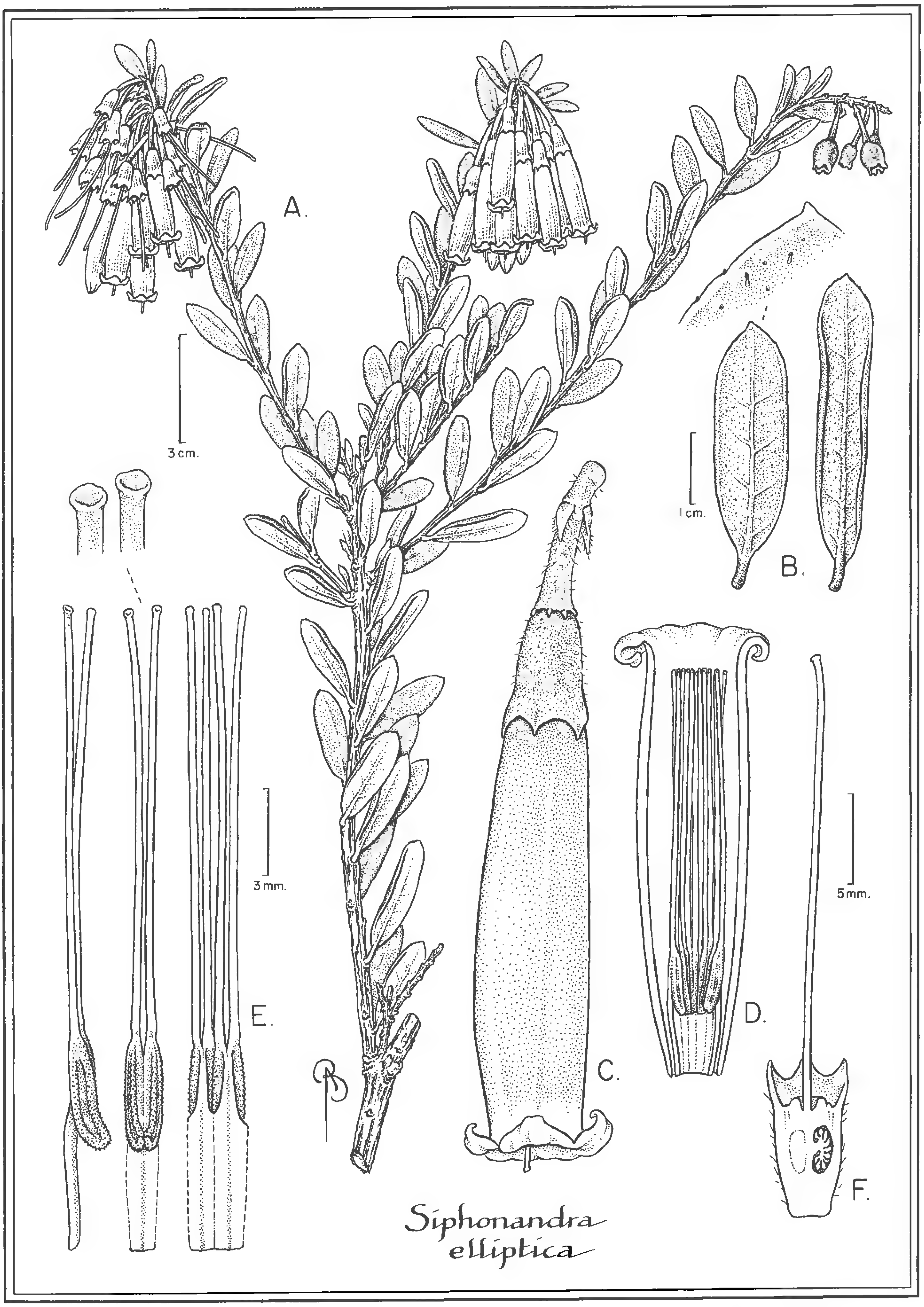

Fig. 3. *Siphonandra elliptica* (Ruiz & Pav. ex G. Don) Klotzsch. A. Habit. B. Leaf variation showing lower surfaces with details of apical portion. C. Flower showing pedicel, bracteoles, calyx, and corolla. D. Longitudinal section of corolla showing position of stamens. E. Stamens showing lateral, ventral, and dorsal views with details of terminal dehiscence pores. F. Longitudinal section of calyx. (A, B-left leaf drawn from *Luteyn et al. 15431*; B-right leaf from *Luteyn & Lebrón-Luteyn 6396*; C-F from *Luteyn et al. 15456*).

glabrous, the thecae incurved and sometimes setose at base, ca. 4–5 mm long, the tubules 13–18 mm long, less than 0.4 mm diam; style about as long as corolla or slightly exserted, the stigma peltate. **Berry** cylindric- to elliptic-ovoid, glabrous to sparsely pilose, to 10–12 mm long, the calyx limb decurrent.

Distribution (Fig. 2).—Common from Peru (Dpts. Amazonas, Apurímac, Cusco, Pasco, Puno) into Bolivia (Dpt. Cochabamba: Prov. Chapare and Dpt. La Paz: Provs. Bautista Saavedra, Franz Tamayo, Inquisivi, Larecaja, Murillo, Nor Yungas, Sud Yungas). Found growing in montane cloud forest, shrub vegetation on sandstone, wet puna, bosque siempreverde, bosque húmedo montano de las yungas, ceja de montaña, at elevations of 2200–4000 m. Flowering in Feb, Mar, Apr, May, Jun, Jul, Sep, Oct, Dec; fruiting in Jun, Dec. Common to abundant.

Representative specimens examined: **PERU. Amazonas:** Chachapoyas, *Weigend et al. 2000/876* (F, NY); *Luya et al. 8843* (USM); near Molinopampa, *van der Werff et al. 14894* (MO); Laguna de Pomacochas, *van der Werff et al. 15822* (MO). **Apurímac:** Pinkos river, *Weberbauer 5861* (F). **Cusco**: Cosñipata, *Weberbauer 6929* (B+, F, US); Cerro de Cusilluyoc, *Pennell 13857* (F, NY, US); La Convención, *Dudley 11124* (USM); *Huamantupa & Huamantupa 4440* (CUZ, MO); Paucartambo, *Cano 3117* (USM); *Croat 78186* (MO); *Soukup 383* (F); Accanaco, *West 7047; Balls 6704* (BM, K, NY, US), *6705; Cano 3117* (USM), *3174* (USM), *3660* (USM), *4520* (USM); *Cano & Aguilar 5157* (USM, F); *Cano & Baldeón 4967* (USM); *Huapalla 136* (USM), *211* (USM); *Luteyn & Lebrón-Luteyn 6396* (F, MO, NY, USM); *Plowman & Davis 5124* (USM); *Tupayachi 30* (MO); Challabamba, *Cano 4339* (USM); Lluntuyoc, *Woytkowski 560* (MOL, USM); Cedrobamba, *Heller 2190* (US); Urubamba, *Metcalf 30749; C. Vargas 3422, 4295* (both US); *F. L. Herrera 3339* (US); *Hoogte & Roersch 1397* (NY); *Keel & Oqueso 439* (AAU, NY); *Funk et al. 3444* (NY, US); *N. Salinas et al. 7620* (CUZ, NY); *Pedraza et al. 1541* (CUZ, NY, USM); *Gentry et al. 23475* (MO, NY); *Luteyn & Lebrón-Luteyn 6377, 6450, 6464* (all at NY, USM); *B. León & Aguilar 2333* (NY, USM); *R. Foster & Wachter 7545* (CUZ, F, NY, USM); *Nuñez 7780* (NY, USM); *Nuñez et al. 8520* (NY, USM). **Junín/Cuzco border:** Satipo/La Convención border, *Boyle et al. 4133* (F, USM), *4138* (F, USM). **Pasco:** Oxapampa, *E. Ortiz 225* (HOXA, MO, USM), *802* (HUSA, USM); *D. N. Smith 2441* (MO), *2516* (MO), *8082* (USM, MO). **Puno:** San Gaván, *Lechler 2276* (K); Tabina, *Lechler 2053* (*S. pilosa* form) (K); Sandia, *Soukup 223; Mathews 884* (BM, K).

BOLIVIA. Eastern Andes, *Pearce 790* (K). **Cochabamba:** Chapare, *Aguilar & Muriel* 1226 (LPB, BOLV); *Atahuachi 876* (BOLV); *Cárdenas 60* (BOLV, US); *Bang 2003* (NY); *J. Steinbach 9529* (BM, G, K, NY, US); *R. Steinbach 646* (US). **La Paz:** Mapiri, *Rusby 2219* (NY), *2036* (B+, BM, F, G, K, NY, US); Yungas, *Rusby 2034*; Bautista Saavedra, *Gutte 458* (LPB); Cocopunco, *Tate 371* (NY); Franz Tamayo, *Maldonado et al. 3210* (LPB); Inquisivi, *Lara 236* (LPB); *Lewis 38496* (LPB, MO, NY), *39358* (LPB, MO, NY), *39421* (LPB, MO), *39719* (LPB, MO), *40940* (LPB, MO); Larecaja, *Krukoff 11466* (F, NY); *Clark 6642* (LPB); *Beck & Ruthsatz 21472* (LPB); between Okara and Ancoma, *Tate 862* (NY); *Luteyn & Dorr 13584* (AAU, BOLV, LPB, NY); *Luteyn et al. 15456* (AAU, BOLV, CAS, CTES, E, LPB, NY, QCNE, TEX); *Gutte & Herzog G458* (LPB); *Pizarro E. 28* (LPB); *Lara D. et al. 236* (LPB); *Clark 6642* (LPB); *Maldonado et al. 3210* (LPB); *Lewis 39719* (LPB); *Solomon & Moraes 11424* (K); Nor Yungas, *Beck 21472* (LPB); *Luteyn et al. 15477* (LPB, NY); *Solomon & Moraes 11424* (LPB, F, MO, NY); Sud Yungas, *Luna-Pizarro 28* (LPB). **Murillo:** *Beck 21551* (LPB); *Luteyn & Dorr 13584* (LPB, BOLV, NY), *Luteyn et al. 15431* (LPB, NY); *Solomon 5230* (MO, NY). **Unknown locality:** *Pearce s.n. (March 1866)* (BM); *C. Troll 1643, 2592* (both B, n.v.). Tablas, 3400 m, *Herzog 2188* (G).

Local name and uses.—willuntuy. Fruits edible, sweet.

Siphonandra elliptica and *S. pilosa* were distinguished only by pubescence persistence of the pedicels and calyces, characters which we do not consider as stable.

3. Siphonandra magnifica Sleumer, Notizbl. Bot. Gart. Berlin-Dahlem 12(112):132–133. 1934. TYPE. BOLIVIA. LA PAZ: Nor Yungas, San Lorenzo-Tola, forest between Tola and San José, 3000 m, 28 Jun 1926 (fl), *C. Troll 2593* [HOLOTYPE: B, destroyed; LECTOTYPE, here designated: US frag. ex B holotype (barcode US00113579)].

Tall **shrubs**; mature stems thick; immature stems angled, glabrous. **Leaves** with blades thick-coriaceous, oblong-ovate, basally narrowed, apically rounded, marginally strongly recurved, obscurely and minutely denticulate or entire, the lamina glabrous; pinnately nerved (?), the midrib strongly impressed above and raised beneath, lateral nerves 4–5, arcuate-ascending, joined at margin, impressed above and often raised beneath; petioles thick, 5 mm long. **Inflorescences** 3–6-flowered; rachis short, hardly 5 mm long, or almost none; floral bract unknown; pedicels thick, glabrous; bracteoles basal, ovate-deltate, acute, ca. 3 mm long. **Flowers** with calyx campanulate, ca. 9 mm long, glabrous, the tube densely bearing squamiform, carnose warts, the limb erect-spreading, the lobes broadly deltate, acute, ca. 1.5 mm long; corolla cylindric, thick-carnose, 3.5–3.7 cm long, 7–8(–9) mm diam., glabrous, the lobes triangular, ca. 2 mm long, reflexed; **stamens** slightly shorter than corolla, ca. 3 cm long, the filaments distinct, often puberulent, ca. 6 mm long, the anthers ca. 2.6 cm long, the thecae subpapillose; style thick, glabrous, ca. 3.5 cm long. **Berry** not seen.

Distribution (Fig. 2).—Endemic to Bolivia (La Paz) and known only from the type. Rare and endangered.

Siphonandra magnifica is herewith maintained despite the fact that the type and only specimen was destroyed during World War II. Sleumer (1934: 133) mentioned that it "surpasses both species as yet known [*S. elliptica* and *S. pilosa*] in all dimensions", but differed from *S. elliptica* by the very short, often indistinct rachis, the very large corolla, the hairy filaments, and the calyx which was covered with fleshy squamules.

NEW SPECIES

4. Siphonandra nervosa Luteyn & E.M. Ortiz, sp. nov. (**Fig. 4**). Type. PERU. Puno: Carabaya, Dtto. Ayapata, near Campamento Chacayage, 13°45.8'S, 70°13.11'W, ca. 2600 m, 10 Mar 2004 (fl), *S. Vilca C., K. Arce C., C. Dávalos M, & E. Ortiz V. 62* (holotype: HUSA; isotypes: HAO, NY).

A *Siphonandra elliptica* foliis lanceolatis (non oblongis vel obovatis), majoribus, 3.5–8.5 cm longis (non 3–5.5 cm), apicibus foliorum breviter obtuseque acuminatis (non obtusis vel subacutis), nervis lateralibus prominentibus per laterem 6–8 (non 3–5), inflorescentiis pauci-floris, 3–4-floris (non 5–15-floris), rhachidibus brevioribus, usque 0.7 cm longis (non 1.5–5 cm), pedicellis brevioribus, usque 7 mm longis (non 7–20 mm) differt.

Lianoid, epiphytic **shrubs** with branches to 10 m long; mature stems terete to subterete, ribbed to bluntly angled, short-pilose with white hairs 0.2–0.3 mm long, the bark exfoliating in thin strips; immature stems subterete to bluntly complanate, striate, moderately short-pilose as mature stems; axillary bud scales narrowly ovate, long-acuminate, pseudostipular, ca. 3 mm long, short-pilose to glabrate. **Leaves** with blades coriaceous, lanceolate to elliptic-lanceolate, (3.5–)5.5–9.5 × (1–)1.5–3 cm, basally broadly cuneate, apically short-acuminate, the apex itself blunt, marginally entire, the lamina sparsely short-pilose and ciliate near base otherwise glabrate above, persistently moderately short-pilose along midrib beneath; pinnately nerved with 8–10 secondary veins per side anastomosing near margin, the midrib strongly impressed above and prominently raised beneath, the secondary nerves slightly impressed above and raised beneath causing leaves to appear slightly bullate, the reticulate veinlets obscure on both surfaces; petioles rugose, subterete, canaliculate above, 3–8 mm long, short-pilose. **Inflorescences** to 5-flowered; rachis sharply angled, ca. 3–5 mm long, sparsely short-white-pilose as stems, circumscribed at base by numerous, ovate, apiculate, ciliate bracts to ca. 2.5 mm long; floral bract ovate, acute, ca. 2.5 mm long, ciliate, marginally also with few glandular fimbriae; pedicels striate to sharply angled, 8–11 mm long, densely short-pilose in bud, glabrate; bracteoles located medially, opposite to subopposite, ovate, long-acuminate, ca. 2–3.5 mm long, marginally glandular-fimbriate, ciliate. **Flowers** with calyx 7–9 mm long, moderately to densely short-pilose, the tube cylindric, terete, 4.5–6.5 mm long, the limb campanulate, 2–4 mm long, the lobes deltate, short-apiculate, ca. 1.5–2 mm long; sinuses broadly rounded; corolla carnose (when fresh), cylindric, conspicuously 5-angled (when fresh), 22–26 mm long, ca. 5–6 mm diam., glabrous, red (when fresh), the lobes erect, deltate, acute, 1.7–2 mm long, yellow to greenish-yellow (when fresh); **stamens** nearly equaling corolla, 20–21 mm long, the filaments connate, 4–4.5 mm long, glabrous, the anthers 17–18 mm long, the thecae 4.8–5 mm long, strongly papillose, the tubules 12.5–13.5 mm long, the pores 0.2 mm diam.; style slightly exserted, glabrous. **Berry** not seen.

Distribution (Fig. 2).—Endemic to southern Peru (Puno) and known only from the type, collected in heavily-disturbed, mature montane forest along a river margin, at ca. 2600 m elevation. Endangered due to its proximity to gold mining and road building activities.

Siphonandra nervosa is characterized by its comparatively large, lanceolate leaf blades with prominent brochidodromous venation, few-flowered inflorescences, short rachis, pedicels and corolla, and connate staminal filaments. When fresh the corolla is 5-angled and red with yellowish lobes. Morphologically it is most similar to *S. elliptica*, differing primarily in the characters mentioned in the key.

5. Siphonandra santa-barbarense Luteyn & E.M. Ortiz, sp. nov. (**Fig. 5**). Type. PERU. Pasco: Oxapampa, Dtto. Huancabamba, Sector Sta. Bárbara, Parque Nacional Yanachaga-Chemillén, source of the Quebrada Cueva Blanca, 10°21'23"S, 75°39'20"W, 3420–3510 m, 16 Aug 2005 (fl), *E. Ortiz V., S. Vilca C., C. Arias C., S. Shuña S. & H. Cristóbal E. 807* (holotype: HUSA; isotypes: HOXA, MO, NY, USM).

A *Siphonandra magnifica* rhachidibus longioribus, 12–25 mm longis (non usque 5 mm), tubo calycis protuberationibus verrucatis carente, corolla breviori, 18–26 mm longa (non 35–37 mm) differt.

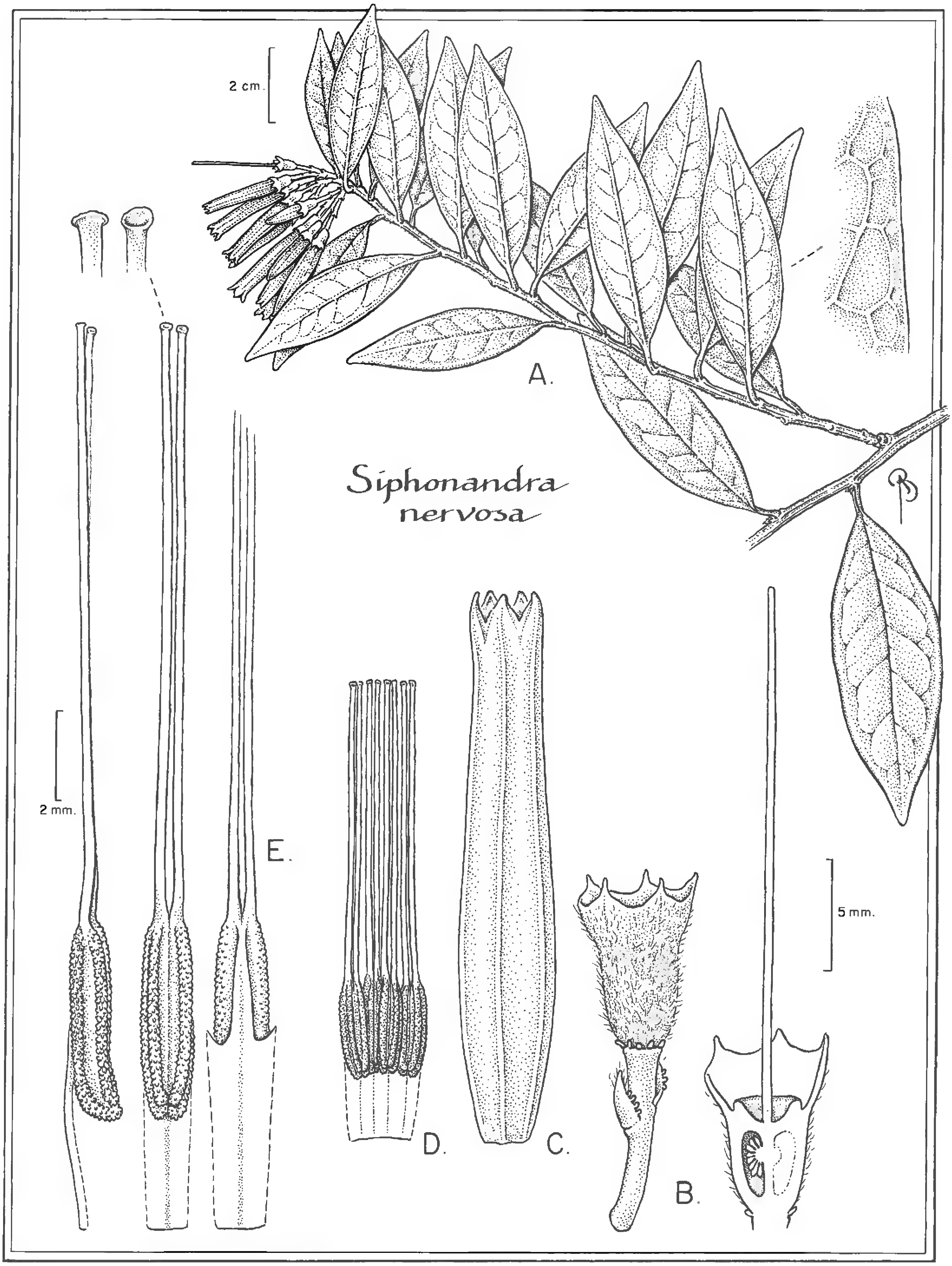

Fig. 4. *Siphonandra nervosa* Luteyn & E.M. Ortiz. **A.** Habit with details of leaf venation and margin beneath. **B.** Flower showing pedicel, bracteoles, and calyx (left) and longitudinal section of calyx (right). **C.** Corolla showing ribs. **D.** Stamens (4) showing connation of filaments and position with regards to corolla (C). **E.** Stamens showing lateral, ventral, and dorsal views with details of terminal dehiscence pores. (Drawn from type collection).

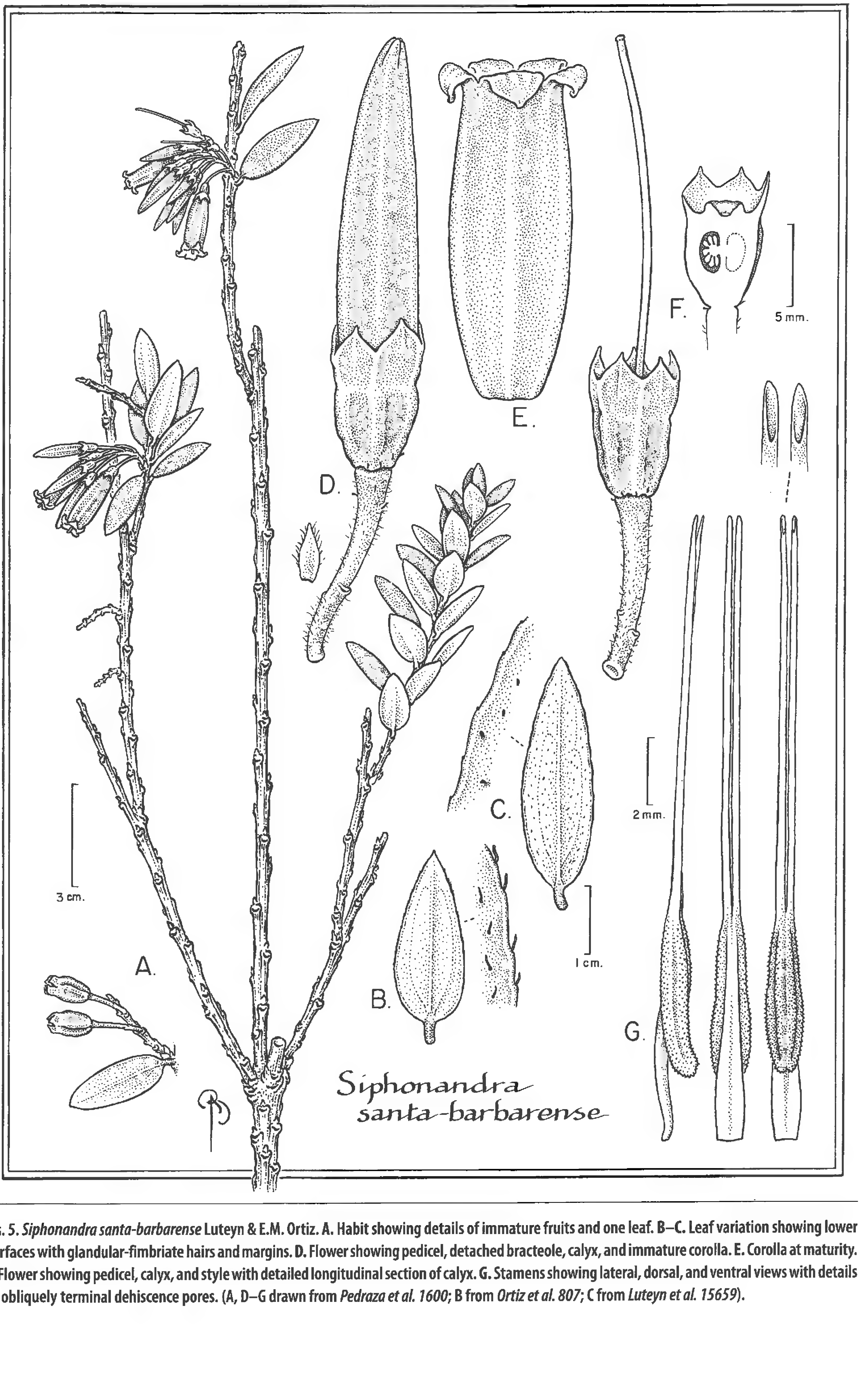

Fig. 5. *Siphonandra santa-barbarense* Luteyn & E.M. Ortiz. A. Habit showing details of immature fruits and one leaf. B–C. Leaf variation showing lower surfaces with glandular-fimbriate hairs and margins. D. Flower showing pedicel, detached bracteole, calyx, and immature corolla. E. Corolla at maturity. F. Flower showing pedicel, calyx, and style with detailed longitudinal section of calyx. G. Stamens showing lateral, dorsal, and ventral views with details of obliquely terminal dehiscence pores. (A, D–G drawn from *Pedraza et al. 1600*; B from *Ortiz et al. 807*; C from *Luteyn et al. 15659*).

Terrestrial or epiphytic **shrubs** to 4 m tall; mature branches terete to subterete, glabrous, the bark separating into thin, longitudinal strips, not exfoliating; vegetative bracts (at base of new twigs) membranous, suborbicular, 3–5 × 2.5–6 mm, basally articulate, truncate, short-acuminate, fimbriate, glabrous; immature branches subterete to ribbed, glabrous to moderately puberulent, the nodes swollen; axillary bud scales 2, valvate, coriaceous, ovate, 1.5–5 × ca. 0.7–1.5 mm, apparently basally continuous thus persistent, long-acuminate, pseudostipular, ciliate to glandular-fimbriate, glabrous. **Leaves** with blades rigidly coriaceous, ovate-oblong, ovate to lanceolate, 2–4 × (1–)1.2–1.8 cm, basally rounded to short-attenuate, apically acute to subacute, sometimes shortly acuminate, also sometimes sharply mucronate, marginally crenate, plane, glabrous above, glandular fimbriate beneath with hairs ca. 0.4 mm long; obscurely 3(–5)-plinerved, the midrib impressed above and raised beneath, more prominent in the proximal 1/3 of the lamina, the lateral nerves slightly impressed above and obscure beneath, the reticulate veinlets slightly impressed above; petioles subterete, slightly flattened dorso-ventrally, rugose, 3–5 mm long, 1–2 mm diam., glabrous to moderately puberulent. **Inflorescences** racemose to subcorymbose, 10–22-flowered; inflorescence bracts membranaceous, ovate, 3 × 2–2.5 mm, basally articulate, apically rounded, entire, glabrous; rachis subterete to ribbed, 12–25 mm long, ca. 2 mm diam., puberulent; floral bract membranaceous, oblong, 5 × 1.5 mm, basally articulate, apically obtuse to rounded, entire, glabrous; pedicels terete, 10–17 mm long, ca. 1 mm diam., puberulent, also with few, scattered, glandular fimbriae distally; bracteoles caducous to persistent, located in proximal 1/3–1/2 of the pedicel, membranaceous, lanceolate, 4 × 1.5 mm, basally articulate, apically acuminate, ciliate to marginally glandular-fimbriate, glabrous. **Flowers** slightly zygomorphic; calyx 6–10 mm long, glabrescent, pink when fresh, sometimes obscurely articulate with pedicel, the tube obconic, 5-ribbed (broadly when fresh), 3.5–6 mm long, ca. 4 mm diam., the limb campanulate, ca. 3–4 mm long, glabrous, the lobes deltate, apiculate to acuminate, 1.2–2.5 mm long; sinuses rounded to subacute; corolla tubular, pentagonal, slightly broadest in the middle, carnose especially along the angles, 18–26 mm long, 6–8.5 mm diam., glabrous, rose-red, the lobes erect to reflexed, deltate, acute to subacute, 2–3.5 mm long, glabrous, externally rose-red, internally whitish; **stamens** 10–20 mm long, the filaments distinct, 3–4 mm long, glabrous, the anthers ca. 17–18 mm long, the thecae tubular with the base shortly incurved and tapering into the tubules distally, 5–6 mm long, slightly papillose, the tubules distinct, 11–13 mm long, dehiscing by an oval, subterminal pore 0.5–1 mm long; nectariferous disc pulvinate, glabrous; style 20–24 mm long, the stigma punctiform. **Berry** immature, obconic, 5-ribbed, 10 mm long, 6 mm diam., glabrous, greenish-red.

Distribution (Fig. 2).—Endemic to the upper limit of montane cloud forest, in elfin forest patches in sheltered areas, alternating with puna grasslands, at elevations of 3400–3600 m. Rare and probably endangered.

Additional material examined: **PERU. Pasco:** Oxapampa, Dtto. Huancabamba, Santa Bárbara, 10°20'35"S, 75°39'0"W, 3400–3500 m, 25 Jan 2004 (bud, fl), *R. Vásquez et al. 29084* (HOXA, HUT, MO, USM); 10°21'24.5"S, 75°39'27.4"W, 3450 m, 9–13 Jun 2006 (fl), *Luteyn et al. 15659* (AAU, COL, CUZ, F, HUSA, MO, NY, USM), *Pedraza et al. 1600* (COL, CUZ, F, HUSA, K, MO, NY, USM).

Siphonandra santa-barbarense is characterized by its flat, marginally crenate, obscurely plinerved leaves with sharply mucronate tips, relatively long rachis, many-flowered inflorescences, articulate (sometimes inconspicuously) calyx, and staminal dehiscence by obliquely subterminal, elongate pores. The type was also found growing in the vicinity of *S. elliptica*.

EXCLUDED TAXA

Siphonandra mexicana Turcz. =*Rondeletia mexicana* (Turcz.) Standley [Rubiaceae].

ACKNOWLEDGMENTS

JLL thanks NSF for funds for his field work and to support travel to NY for EMO. EMO thanks the Missouri Botanical Garden for funding for his fieldwork in Peru; also to Michael O. Dillon and the Botany Department, The Field Museum, for support from the Timothy C. Plowman Latin American Research Award. We also thank Wayt Thomas for supplying the GIS layers for the America's Basemap.

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Numerical List of Taxa

1. *Siphonandra boliviana* Luteyn
2. *Siphonandra elliptica* (Ruiz & Pav. ex G. Don) Sleumer
3. *Siphonandra magnifica* Sleumer
4. *Siphonandra nervosa* Luteyn & E.M. Ortiz
5. *Siphonandra santa-barbarense* Luteyn & E.M. Ortiz

List of Exsiccatae (*recognized type collection numbers in boldface)

Aguilar, B. & Muriel, 1226 (2)
Atahuachi, M., 876 (2)
Balls, E. K., 6704, 6705 (2)
Bang, M., 2003 (2)
Beck, S., 21472, 21551 (2)
Boyle, B. et al., 4133, 4138 (2)
Cano, A., 3117, 3174, 3494, 3660, 4330, **4339**, 4520 (2)
Cano, A. & Aguilar, 5157 (2)
Cano, A. & Baldeón, 4967 (2)
Cárdenas, M., 60 (2)
Clark, J.L., 6642 (2)
Croat, T., 78186 (2)
Díaz, C. & Peña 8843 (2)
Dudley, T., 11124 (2)
Ellenberg, H., 4852 (2)
Foster, R. & Wachter, 7545 (2)
Funk, V. et al., 3444 (2)
Gay, Cl., s.n., 709 (2)
Gentry, A. et al., 23475 (2)
Gutte, P., 458 (2)
Heller, 2190 (2)
Herzog, B., **H200 (1)**
Herzog, Th., 2188 (2)
Herrera, F. L., 3339 (2)
Hoogte & Roersch, 1397 (2)
Huamantupa, I. & Huamantupa, 4440 (2)
Huapalla, N. et al., 136, 211 (2)
Keel, S. & Oqueso, 439 (2)
Krukoff, B.A., 11466 (2)
Lara, D., 236 (2)
Lechler, W., **2276**, 2053 (2)
León, B. & Aguilar, 2333 (2)
Lewis, M., 38496, 39358, 39421, 39719, 40940 (2)
Luna-Pizarro, E., 28 (2)
Luteyn, J.L. & M. Lebrón-Luteyn, 6377, 6396, 6450, 6464 (2)
Luteyn, J.L. et al., 13584, 15431, 15456, 15477 (2); 15659 (5)
Maldonado, C. et al., 3210 (2)
Mandon, G., 549 (2)
Mathews, 884 (2)
Messinger, W., et al. 407 (2)
Metcalf, R.D., 30749, (2)
Nuñez V., P., 7780 (2)
Nuñez V., P. et al., 8520, 8522 (2)
Ortiz, E.M. et al., 225, 802 (2), **807 (5)**
Pearce, R.W., 790 (2)
Pedraza, P. et al., 1541 (2); 1600 (5)
Pennell, F. W., 13857 (2)
Peyton, B. & S. T. Peyton, 318, 771 (2)
Ruiz L., H. & J.A. Pavón, **s.n. (2)**
Rusby, H.H., 2034, 2036, 2219 (2)

Salinas, N. et al., 7620 (2)
Smith, D.N., 2441, 2516, 8082 (2)
Solomon, J.C., 5230, 11424 (2)
Solomon, J.C. & M. Moraes, 11424 (2)
Soukup, J., 223, 383 (2)
Steinbach, J., 9529 (2)
Steinbach, R., 646 (2)
Tate, G.H.H., 371, 862 (2)
Troll, C., 1643, 2592 (2), **2593 (3)**
Tupayachi, A., 30 (2)
Van der Werff, H. et al., 14894, 15822 (2)
Vargas, C., 3422, 4295 (2)
Vásquez, R. et al., 29084 (5)
Vilca, S. et al., **62 (4)**
Weberbauer, A., 740, 5861, 6929 (2)
Weddell, H. Alg., 4711 (2)
Weigend, M. et al., 2000/876 (2)
West, J., 7047 (2)
Woytkowski, F., 560 (2)
Zimmerer, K.S., 114 (2)

BOOK REVIEW

Richard K. Rabeler. 2007. **Gleason's Plants of Michigan.** (ISBN 978-0-472-03246-4, pbk.). University of Michigan Press, 839 Greene Street, Ann Arbor, Michigan 48104, U.S.A. (**Orders:** www.pres.umich.edu, robert.pierce@perseusbooks.com, University of Michigan Press, c/o Perseus Distribution, 1094 Flex Drive, Jackson, Tennessee 38301, U.S.A., 1-800-343-4499 Ext. 165, 1-877-364-7062 fax). $24.95, 400 pp., b/w drawings, terminology, glossary, indices to plant names and family names, 5" × 7".

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Richard K. Rabeler has revised the early 1900s *Gleason's Plants of Michigan*. This revised text is an excellent field guide and designed to be used as such, focusing on the ability of the user to view plant characteristics by sight or with a hand lens, and providing a small ruler in the back for field use. There is a helpful illustrated terminology section in the beginning of the book and a glossary in the back of the text. This guide utilizes a dichotomous key to identify first to groups (woody plants, monocots, dicots, and unusual plants-such as aquatic or parasitic plants), then to family and eventually to species. Rabeler provides a handy quick family index for when the user has prior knowledge of the family. The guide is sprinkled with black and white line drawings of many of the plants included in the guide, as well as small boxes of information related to species as they occur in Michigan and quick field plant characteristics to aid with identification.

Overall, Rabeler's revised *Gleason's Plants of Michigan* is a wonderful field text for plant enthusiasts, students, and taxonomists who are involved in field identifications. The guide has many helpful features for the amateur—illustrated terminology and line drawings, as well as helpful references such as the family quick reference for the more seasoned taxonomist. Most beneficial is that this guide is corrected and updated from the 1918 version of the guide and is quite a bit easier to carry than the unequivocally most comprehensive flora of the region, Edward G. Voss's *Michigan Flora* (3 volumes, 1837 pp.!).—*Lee Luckeydoo, Botanical Research Institute of Texas, 500 East 4th Street, Fort Worth, Texas 76102-4025, U.S.A.*

FOLIA TAXONOMICA 4. CONSPECTUS OF *MYRIOPUS* (HELIOTROPIACEAE: BORAGINALES) IN THE GUIANA SHIELD

Christian Feuillet

Department of Botany, MRC-166
Smithsonian Institution
P.O. Box 37012
Washington, DC 20013-7012, U.S.A.
feuillec@si.edu

ABSTRACT

The conspectus lists the five taxa of newly resurrected *Myriopus* Small (Heliotropiaceae) present in the Guiana Shield flora. The synonymy and four new combinations are included.

RÉSUMÉ

Le conspectus donne les cinq taxa du genre récemment reconnu *Myriopus* Small (Heliotropiaceae) présents dans la flore du Bouclier Guyanais. La synonymie et quatre combinaisons nouvelles sont incluses.

In the past few years, a better understanding of the relationship between taxa of the Boraginales was the focus of several papers through the re-examination of old and the gathering of new morphological data and the analysis of molecular data (Diane et al. 2002, 2003; Hilger & Diane 2003; Gottschling et al. 2005; Miller & Gottschling 2007). Familial and generic limits have been re-considered. In the preparation of the treatment of the Boraginales for the Flora of the Guianas, I had to decide whether I should follow the traditional taxonomy as used for the Boraginaceae treatments in "Flora of Venezuelan Guayana" (Miller et al. 1997) and in "Checklist of the Plants of the Guiana Shield" (Feuillet et al. 2007) or to adapt it to reflect the changes proposed since 1997 in the systematic of this group. As it is often the case with work in progress, some proposals should be adopted, like the separation of *Varronia* P.Br. from *Cordia* L. (Cordiaceae) and of *Myriopus* Small from *Tournefortia* L. (Heliotropiaceae), when other aspects need further work including more species in the data sets, like the split of *Heliotropium* L. and its relation with *Tournefortia* s.s. Currently less than 10% of the species have been analyzed in the whole Heliotropiaceae and it is likely that some major clades of *Heliotropium* s.l. and *Tournefortia* s.s. are missing from the data sets.

The part of the new classification of the Heliotropiaceae proposed by Diane and her colleagues that is most likely to resist larger sampling is the separation of *Myriopus* from *Tournefortia* and its standing as a sister group to *Heliotropium* s.l. and *Tournefortia* s.s. It was pointed out by Johnston (1930) that his new *Tournefortia* sect. *Cyphocyema* I.M. Johnst. was distinct from the core of *Tournefortia*. He suggested on a morphological basis that the two sections of *Tournefortia* were closer to other genera than to each other. Small (1933) included two species of sect. *Cyphocyema* in his new genus *Myriopus* and said there was more Neotropical species. The morphological characters that separate *Myriopus* apart from *Tournefortia* s.s. are its elongated corolla lobes, narrow with involute margin, its anthers connate and always hairy at apex, its drupoid fruits distinctly lobed and not dividing into mericarpids, its four 1-seeded endocarpids that are strongly curved, and its curved embryos (Johnston 1930; Diane et al. 2002). The molecular and morphological data sets used by Diane et al. (2002, 2003), Hilger and Diane (2003) confirmed the deep separation between *Tournefortia* sect. *Cyphocyema* and most of the Heliotropiaceae. The *Cyphocyema/Myriopus* branch is supported by bootstrap percentages of 100% in all trees. Logically Diane et al. (2002) proposed to use *Myriopus* Small as a generic name for the species of *Tournefortia* sect. *Cyphocyema*. The conspectus presented below is listing the taxa of *Myriopus* present in the Guianas (Guyana, Surinam & French Guiana) and the Venezuelan Guayana (Amazonas, Bolivar & Delta Amacuro), the most part of a region often referred to as

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the Guiana Shield or Guayana Shield. Four taxa from the Guianas did not have a name in *Myriopus* and needed a new combination.

KEY TO THE GENERA OF HELIOTROPIACEAE IN THE GUIANAS

1. Herbs. Fruits usually dry when fresh ____ **Heliotropium**
1. Shrubs or lianas. Fruits fleshy when fresh.
   2. Corolla lobes linear or long acuminate. Fruits evidently lobed, obscurely bicarpellate, consisting of 4 similar 1-seeded nutlets. Embryos curved. ____ **Myriopus**
   2. Corolla lobes broad and rounded. Fruits obscurely if at all lobed, evidently bicarpellate, breaking up into 1- or 2-seeded irregular nutlets. Embryos straight ____ **Tournefortia**

Myriopus candidulus (Miers) Feuillet, comb. nov. Basionym: *Messerschmidia candidula* Miers, Ann. Mag. Nat. Hist. ser. 4, 2:202. 1868. *Tournefortia candidula* (Miers) I.M. Johnst., Contr. Gray Herb. 92:84. 1930. Type: BRAZIL: *Gardner1078* (holotype: BM; isotypes: K, NY).

= *Tournefortia lanuginosa* Vaupel, Notizbl. 6:183. 1914. Type: BRAZIL: *Ule 9097* (holotype: BD (n.v.); isotype: K)

Myriopus maculatus (Jacq.) Feuillet, comb. nov. Basionym: *Tournefortia maculata* Jacq., Enum. Syst. Pl. 14. 1760; Select. Stirp. Amer. Hist. 47. 1763. Type: COLOMBIA: Cartagena, "Habitat Carthagenae in arbustis & sepibus" (n.v.).

= *Tournefortia syringaefolia* Vahl, Symb. Bot. 3:23. 1794. Type: FRENCH GUIANA: *von Rohr s.n.* (holotype: C (n.v.); isotype: BM).

= *Tournefortia peruviana* Poiret, Encycl. Suppl. 4:425. 1816. *T. volubilis* sensu Ruiz & Pav. (non L. 1753), Flor. Per. 2:24, tab. 148. 1799. *T. scandens* Willd. (non Mill. 1768), Enum. Pl. 1:188. 1809. Type: PERU. Pasco. Pozuzo, *Ruiz & Pavón s.n.* (holotype: MA (n.v.); isotype: US). The US specimen in the type collection, under *T. scandens* Willd., has a label with handwritten "*Tournefortia volubilis* Fl. Peruv. 2 Zap. 48 ..." and " ex herbario Fl. Peruv. anno 1828," and off that label, Killip's handwriting, "Type of *T. volubilis* R. & P. = *T. peruviana* Poir." and "Part of type ex herb. Madrid Ruiz & Pavon."

= *Tournefortia surinamensis* A. DC., Prodr. 9:526. 1845. Type: SURINAM. *Hostmann 951* (holotype: G-BOISS).

= *Tournefortia hostmannii* Kl. ex Schomb., Fauna Fl. Brit. Guiana 1151. 1848, nom. nud., based on *Hostmann 285* (BD, BM, K, P).

Myriopus paniculatus (Chamisso) Feuillet, comb. nov. Basionym: *Tournefortia paniculata* Chamisso, Linnaea 4:468. 1829. Type: *Sellow* (B, extant?).

Myriopus paniculatus var. **spigeliiflorus** (A. DC.) Feuillet, comb. nov. Basionym: *T. spigeliaeflora* A. DC., Prodr. 9:525. 1845. *Tournefortia paniculata* Chamisso var. *spigeliiflora* (A. DC.) I.M. Johnst., J. Arnold. Arbor. 16:49. 1935. Type: GUYANA: *Rob. Schomburgk ser. 2, 427* (holotype: G-BOISS; isotypes: BM, K, P).

Myriopus volubilis (L.) Small, Man. S.E. Fl. 1131. 1933. *Tournefortia volubilis* L., Sp. Pl. 140. 1753. Lectotype: "Bryonia nigra fruticosa, racemi ramulis varie implicitis, atq. caudae scorpionis instar in se contortis, baccis albis una vel altera nigra macula notatis" in Sloane, Voy. Jamaica 1: t. 143, f. 2. 1707.

= *Tournefortia floribunda* sensu Schomburgk, Fauna u. Fl. Brit. Guian. 1084. 1848. non Kunth 1818.

KEY TO THE GUIANAN SPECIES

1. Leaves densely white-tomentose on lower surface, grayish green pubescent on upper surface; inflorescence terminal with short lateral branches, appearing as a very contracted panicle; fruits white-pubescent. (Guyana) ____ **M. candidulus**
1. Leaves glabrous or pubescent, never white-tomentose; inflorescence terminal or axillary, paniculate with long lateral branches or a glomerulate with short branches; fruits never white-pubescent.
   2. Corolla tube 1.5-2.5 mm long, constricted at throat, lobes linear, nearly as long as the tube; fruit white. (Guyana, Surinam, French Guiana) ____ **M. volubilis**
   2. Corolla tube 3-8 mm long, not constricted at throat, lobes broadened below middle, acuminate, half as long as the tube or less; fruit yellowish, pedicel thickening in fruit.
      3. Leaves, young stems and inflorescence sparsely short strigose, or glabrous; corolla lobes narrow triangular to linear. (Guyana, Surinam, French Guiana) ____ **M. maculatus**
      3. Leaves, young stems and inflorescence evidently and usually abundantly hairy; corolla lobes triangular, long acuminate. (Guyana, Surinam, French Guiana) ____ **M. paniculatus** var. **spigeliiflorus**

ACKNOWLEDGMENTS

I would like to thank the reviewers for their suggestions regarding the introduction and the curators of the herbaria CAY, F, NY, P and U for lending the material in their care. This is number 134 in the Smithsonian's Biological Diversity of the Guiana Shield Program publication series.

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BOOK REVIEWS

Beth Judy. 2007. **Medicinal Plants of North America: A Flora Delaterre™ Coloring Book.** (ISBN 978-0-9792302-0-2, pbk.). Flora Delaterre™ Productions, P.O. Box 8474, Missoula, Montana 59807, U.S.A. (**Orders:** www.floradelaterre.com, 1-406-728-2977). $12.00, 32 pp., 33 b/w line drawings, 8.5" × 11".

Medicinal Plants of North America: A Flora Delaterre™ Coloring Book is a fun and educational activity book for any young explorer. The book presents a black and white line drawing for coloring and descriptive text for 14 medicinal plants. The author wisely includes a disclaimer that this book is for "knowledge only". Information about each plant includes some ecological information, plant description, brief explanation of medicinal value, and fun facts about the plant. Additional ideas for ways to learn more about medicinal plants are included on the last page. A great activity book for a budding botanist.—*Lee Luckeydoo, Botanical Research Institute of Texas, 500 East 4th Street, Fort Worth, Texas 76102-4025, U.S.A.*

Max Schnepf and Craig Cox (eds.). 2007. **Managing Agricultural Landscapes for Environmental Quality: Strengthening the Science Base.** (ISBN 978-0-9769432-4-2, pbk.). Soil and Water Conservation Society, 945 SW Ankeny Road, Anken, Iowa, U.S.A. (**Orders:** www.swcs.org, http://store.swcs.org, 1-515-289-2331, 1-515-289-1227 fax). $32.00, 196 pp., b/w line drawings, charts, graphs, index, 7" × 10".

In October of 2006, the Soil and Water Conservation Society held a meeting in Kansas City called "Managing Agricultural Landscapes for Environmental Quality". Afterward, the topics that made up their multidisciplinary workshop were turned into a book of the same name. Among the topics included in the book are what we should measure and how to account for environmental effects. Also discussed are methods of environmental management research at landscape and watershed scales, targeting within landscapes and watersheds to improve conservation effectiveness, realistic expectations about timing between conservation implementation and environmental effects, and research information needs. Each topic also includes a summary of main themes and concepts that developed during roundtable discussions held at the workshop.

This book presents the reader with an in-depth and current view of management approaches and perspectives, including case studies from various people involved in conservation practices and policy regarding conservation on varying scales. Papers included within the main topics present information in a practical and well-referenced format. The book offers readers some interesting information about how conservation concepts and environmental valuation, scale, research approaches, management practices, and policies can all interact. The book is valuable for those with an interest in evaluating conservation management practices on environmental quality in agricultural landscapes.—*Lee Luckeydoo, Botanical Research Institute of Texas, 500 East 4th Street, Fort Worth, Texas 76102-4025, U.S.A.*

FOLIA TAXONOMICA 5. A NEW NAME FOR *PASSIFLORA HETEROPHYLLA* (PASSIFLORACEAE) FROM CUBA AND HAITI

Christian Feuillet

Department of Botany, MRC-166
Smithsonian Institution
P.O. Box 37012
Washington, D.C. 20013-7012, U.S.A.
feuillec@si.edu

John M. MacDougal

Division of Arts and Sciences
Harris-Stowe State University
3026 Laclede Avenue
St. Louis, Missouri 63103, U.S.A.
threebrane@sigmaxi.net

ABSTRACT

The name *Passiflora heterophylla* Lam. does not have priority over *Passiflora heterophylla* Dryand. and the taxon does not have another name available. The new name **Passiflora insueta** is proposed for that species.

RÉSUMÉ

Le nom *Passiflora heterophylla* Lam. n'a pas priorité sur *Passiflora heterophylla* Dryand. et le taxon n'a pas d'autre nom disponible. Le nouveau nom **Passiflora insueta** est proposé pour cette espèce.

Both Dryander (1789) and Lamarck (1789) published a taxon named *Passiflora heterophylla*. According to TL-2 (Stafleu & Cowan 1976), Dryander's name was published between Aug 7 and Oct 1, while Lamarck's name was from Oct 19 (Stafleu & Cowan 1979), thus giving Dryander's name priority. Killip (1938) accepted Lamarck's species and name but cited Dryander's as a synonym under *P. suberosa* L. as "*Passiflora heterophylla* Dryand. in Ait. Hort. Kew. 3:309. 1789, not *P. heterophylla* Lam." Dryander's species is now considered a synonym of *P. pallida* L. in subgen. *Decaloba* supersect. *Cieca* (Medic.) J.M. MacDougal & Feuillet (Porter-Utley 2003) and *P. heterophylla* Lam. is a good species without a valid name and without synonym. *Passiflora heterophylla* "Jacq., Hort. Schoenbr. t. 181. 1797" is Dryander's species because Jacquin credited "Ait. kew. vol. 3. pag. 309." There is no name available for the taxon currently called *P. heterophylla* Lam., so we propose the following new name:

Passiflora insueta Feuillet & MacDougal, nom. nov. Basionym *Passiflora heterophylla* Lam., Encycl. 3:41. 19 Oct 1789, non Dryand. 7 Aug–1 Oct 1789. (including the Latin diagnosis). Type: HAITI: Anses à Pitres, Pointe Icaque, *Plumier? s.n.* (holotype: P!).

Passiflora insueta belongs in subgen. *Decaloba* supersect. *Multiflora* (Small) J.M. MacDougal & Feuillet (Feuillet & MacDougal 2003). The leaf blades of this poorly known species are lobed nearly to the base and the lobes themselves are unlobed or lobed in their apical half.

Etymology.—The epithet comes from the Latin adjective "insuetus" meaning "unusual" in reference to the leaf shapes.

Passiflora insueta is known from Haiti and western Cuba.

ACKNOWLEDGMENT

We are very grateful to the directors and curators who sent photographs and allowed us to work on the collections in their care at P and MO. The review comments of Kristen E. Porter-Utley are greatly appreciated.

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FOLIA TAXONOMICA 6. TWO NEW SPECIES OF *BESLERIA* (GESNERIACEAE) FROM THE VENEZUELAN GUAYANA

Christian Feuillet

Department of Botany, MRC-166
Smithsonian Institution, P.O. Box 37012
Washington, DC 20013-7012, U.S.A.
feuillec@si.edu

ABSTRACT

Two species of *Besleria* (Gesneriaceae) are described from the state of Amazonas in southeastern Venezuela. **Besleria neblinae** and **B. yatuana** are related to *B. gibbosa* in section *Neobesleria* subsection *Axillares* from which they differ mainly by their leaves strongly unequal in a pair.

RÉSUMÉ

Deux espèces de *Besleria* (Gesneriaceae) sont décrites de l'état d'Amazonas, au sud-est du Venezuela. **Besleria neblinae** et **B. yatuana** sont poches de *B. gibbosa*, section *Neobesleria* subsection *Axillares*, dont elles diffèrent surtout par leurs feuilles très inégales dans une paire.

RESUMEN

Se describen dos especies de *Besleria* (Gesneriaceae) del estado de Amazonas en el sudeste de Venezuela. **Besleria neblinae** y **B. yatuana** son relacionados a *B. gibbosa* en sección *Neobesleria* subsección *Axillares*, del cual difieren principalmente por las hojas que no son iguales en un par.

This paper is the first of a series describing new species of Gesneriaceae from the Venezuelan Guayana. This region of Venezuela includes the states of Amazonas, Bolívar, and Delta Amacuro, totaling 454,000 km^2 that represents 50% of the area of Venezuela. The two new species of the subfamily Gesnerioideae Link described herein belong to *Besleria* L., tribe *Beslerieae* Bartl. & H.L. Wendl., and were collected in the state of Amazonas.

Besleria neblinae Feuillet, sp. nov. (**Fig. 1**). Type: VENEZUELA. Amazonas. Dept. Río Negro: near Cerro de la Neblina, swamp between Río Marawinuma and headwaters of Río Baría, ca. 0°52'N, 66°15'W, 140 m, 8 May 1984, *A. Gentry & B. Stein 47253* (holotype: US; isotype: MO).

Besleriae gibbosae affinis; lamina angustata, valde inaequali, lobis calycis longioribus, angustioribus et hirsutis, dorsali glande parviore differt.

Suffrutescent herb, 0.3–2 m tall, often with spreading, sub-horizontal branches. Stem slender, densely villous. Leaves of a pair mostly unequal: smaller leaves with petioles about 1/5 the length of those of the larger leaves, blades about 1/3 the size of the larger; mature larger leaves with petioles 1.5–4.5 cm, densely villous; blades 9–19 × 3–5.5 cm, lanceolate to elliptic, often asymmetric, base acute to obtuse, occasionally nearly rounded, apex acute to acuminate, margin serrulate and ciliate, both surfaces with appressed trichomes, indumentum loose between veins, dense and spreading on midrib and main veins, 8–12 main veins on each side. Inflorescences sessile, 1–2-flowered; pedicels 3–5 mm long, densely villous. Flowers with calyx hirsute, tube 1.5 mm long, lobes lanceolate, 5.5–6 × 1.2–1.5 mm, attenuate at apex, slightly longer in fruit; corolla white, horizontal in the calyx, glandular puberulent outside, prominently spurred, spur 5–5.5 × 2–3 mm, oblong, rounded, prolonging the tube at base, tube 25–35 mm long, 3 mm wide at base and 6 mm at throat, lobes yellow (fide *Davidse & Miller 26864*), suborbicular, 4 × 4 mm; 4 stamens about 25 mm long, anthers with thecae reniform encircling a round connective; 1 staminode 3 mm long, with a sterile linear anther;

Fig. 1. *Besleria neblinae* Feuillet. Stem with flowers, *Gentry & Stein 47253* (holotype: US); insets, flowers, *id.* (isotype: MO).

dorsal glands fused into one, semi-annular, tongue-shaped, emarginate; ovary superior, ovoid, glabrous, 3 mm long, style 20 mm long, glabrous. Young fruits green, narrowly ovate, long-tapering, 9 x 3 mm.

Distribution.—*Besleria neblinae* grows in wet forests and on hummocks in swamp forests in the southern part of the Municipio Río Negro, Amazonas (Venezuela) near the base of Cerro de la Neblina, at 100–140 m elevation. The Neblina massif is on the border with Brazil and it is possible that populations of this new species are present in nearby Brazil.

Phenology.—Blooming probably not seasonal, documented in February-March, May, July, November.

Besleria neblinae corollas have a spur at the base that prolongs the tube at a 0–20° angle (cf. Fig. 1 inset) and displaces the attachment to the receptacle in a lateral position. According to Morton (1939), this character places *B. neblinae* in sect. *Neobesleria* C.V. Morton. Furthermore, its obsolete inflorescence peduncle and the size of the corolla limb indicate the species belongs to subsect. *Axillares* C.V. Morton, one of the two subsections of sect. *Neobesleria* that remain after five were transferred to the reinstated genus *Gasteranthus* Benth. In the same subsection and from Amazonian Brazil and Venezuelan Guayana, *B. gibbosa* (Poepp.) Hanst. also has white corollas, but *B. neblinae* differs by: 1) the leaf blades which are clearly unequal in a pair (versus equal or subequal) and narrower, 2) the calyx lobes that are longer, narrower, and hirsute (versus glabrous), and 3) the dorsal glands that are smaller. In the specimen *Liesner 17300*, most pairs of leaves are subequal but the smaller petioles are 1/2 as long as the larger ones which is distinctive from B. gibbosa. The collection *Thomas 3396* was made in the same locality and the same day as the type collection, *Gentry & Stein 47253*. Although a different collection (W. Thomas, pers. com.), it is possible that both represent the same population. This species was *Besleria* "sp. B" in Feuillet and Steyermark (1999).

Etymology.—*Besleria neblinae* is named for Cerro de la Neblina near the base of which all the known collections have been made.

PARATYPES: **VENEZUELA. Amazonas. Dept. Río Negro:** at base of Cerro de la Neblina, swamp forest between Río Marawinuma and Río Baría, 0°50'N, 66°09'W, 8 May 1984, *W.W. Thomas 3396* (NY, US); Upper Caño Baría, ca. 0°52'N, 66°15'W, 130 m, 26 Mar 1984, *R. L. Liesner 16964* (MO, US, VEN); 1 km E of Cerro de la Neblina base camp which is on Río Marawinuma, 0°50'N, 66°10'W, 140 m, 25 Feb 1984, *R. L. Liesner 16254* (MO, US, VEN), 25–26 Nov 1984, *R.L. Liesner 17300* (MO, US), 30 Nov 1984, *R. L. Liesner 17382* (MO, US); Upper Río Baría, ca. 0°52'N, 66°15'W, 100 m, 2–3 Jul 1984, *G. Davidse & J. S. Miller 26864* (MO, US, VEN).

Besleria yatuana Feuillet, sp. nov. (**Fig. 2**). TYPE: VENEZUELA. AMAZONAS. Dept. Río Negro: near Cerro de la Neblina, uppermost Río Yatúa, 100–140 m, 7–8 Dec 1953, *B. Maguire, J.J. Wurdack & G.S. Bunting 36729* (HOLOTYPE: US sheet 2195721; ISOTYPE: NY, US sheets 2195722 & 2614591).

Besleriae neblinae affinis; lamina longe acuminata, lobis calycis liberis, longioribus, latioribus et minute appressis-pubescentibus differt.

Suffrutescent herb, 1 m tall, spreading branches. Stem somewhat succulent, appressed-pubescent. Leaves of a pair mostly unequal; smaller leaves with petioles up to 1/4 the length of those of the larger leaves, blades less than 1/2 the length of the larger; mature larger leaf with petioles 3–5 cm, appressed-pubescent; blades 11–20 x 4–6 cm, lanceolate to elliptic, slightly asymmetric, base acute, apex long acuminate, margin serrulate, adaxially glabrous, abaxially glabrous except for the midrib and main veins sparsely appressed-short-pilose, 9–10 secondary veins on each side. Inflorescences sessile, 1–2-flowered; pedicels 3–6 mm long, appressed-pubescent. Flowers with calyx minutely appressed-pubescent, lobes free to base, lanceolate-linear, attenuate at apex, 6–10 x 2.5 mm; corolla horizontal in the calyx, white, sparsely to moderately pilose outside, trichomes with spherical glandular tip, prominently spurred, spur 6 x 4 mm, ovoid-oblong, rounded, prolonging the tube at base, tube 25 mm long, 4 mm wide at base and 2 mm at throat, lobes suborbicular, 5–6 x 1.5 mm; 4 stamens about 2.5 cm long, anthers orbicular-reniform; staminode not seen; dorsal glands fused into one; ovary superior, ovoid, glabrous, 3 mm long. Fruits not seen.

Distribution.—The type collection of *Besleria yatuana* in bloom was made in December in the flooded forests along the upper-most Río Yatúa in the southern part of the Municipio Río Negro, Amazonas (Venezuela).

Besleria yatuana shares with *B. neblinae* the characters that places both of them in subsect. *Axillares.*

FIG. 2. *Besleria yatuana* Feuillet. **Top:** stem showing unequal leaves in a pair, *Maguire, Wurdack & Bunting 36729* (holotype: US); **bottom:** nodes with flowers, *id.* (isotype: US).

It has white corollas like *B. gibbosa* and *B. neblinae*, but differs from the first one in having leaves that are strongly unequal in a pair (versus equal or subequal) and long acuminate (versus acute to acuminate), its longer and appressed-pubescent (versus glabrous) calyx lobes, and its smaller dorsal gland *Besleria yatuana* differs from *B. neblinae* in having the leaf blades adaxially glabrous (versus appressed pubescent), the calyx minutely appressed pubescent (versus hirsute), calyx lobes free to the base, and the slightly shorter corolla tube. *Besleria yatuana* was *Besleria* "sp. C" in Feuillet and Steyermark (1999).

Etymology.—*Besleria yatuana* is named for the Río Yatúa near which the type specimens have been collected.

KEY TO *BESLERIA* SUBSECTION *AXILLARES* IN THE GUIANA SHIELD

1. Corolla not spurred, but sometimes a little saccate at base ______ sect. **Besleria**
1. A spur at the base that prolongs the corolla tube and displaces the attachment to the receptacle in a lateral position. ______ sect. **Neobesleria**
    2. Inflorescence peduncle, much exceeding the pedicel in length ______ subsect. **Pendulae**
    2. Inflorescence peduncle obsolete. ______ subsect. **Axillares**
        3. Leaves in a pair equal or subequal; calyx lobes glabrous ______ **B. gibbosa**
        3. Leaves in a pair, at least the petiole, strongly unequal in a pair; calyx lobes hairy.
            4. Stems, petioles, pedicels, and calyx appressed pubescent; leaf blades glabrous except for the main veins underneath; calyx lobes free to base, 6–10 × 2.5 mm, appressed-pubescent ______ **B. yatuana**
            4. Stems, petioles, pedicels, and calyx densely villous with lax spreading trichomes up to 2 mm long; leaf blades with appressed trichomes; calyx tube 1.5 mm long, lobes 5.5–6 × 1.2–1.5 mm, hirsute ______ **B. neblinae**

ACKNOWLEDGMENTS

I am grateful for the suggestions of Larry Skog, Jim Smith and an anonymous reviewer. I want to thank the curators of the herbaria MO and NY for lending the material in their care, and especially Jim Solomon (MO) and Wayt Thomas (NY) for the information about the collections cited. This paper is published as No. 135 in the Smithsonian's Biological Diversity of the Guiana Shield Program publication series.

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BOOK REVIEW

Roy Morey. 2008. **Little Big Bend: Common, Uncommon, and Rare Plants of the Big Bend National Park.** (ISBN 978-0-89672-613-0, pbk.). Texas Tech University Press, Box 41037, Lubbock, Texas, 79409-1037, U.S.A. (**Orders:** www.ttup.ttu.edu, ttup@ttu.edu, 1-800-832-4042, 1-806-742-2982, 1-806-742-979 fax). $34.95, 329 pp., color photographs, 7.5" × 10".

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An updated guide to the plants of the Big Bend is long overdue. There was the 1951 Park Service *Plants of the Big Bend National Park* by W.B. McDougall and Omer E. Sperry with 190 species and numerous small black and white photos. Barton Warnock's *Wildflowers of the Big Bend Country* with colored photos and very brief descriptions followed in 1970. Since then explorers into the flora of the region have turned to the general guides to Trans-Pecos plants by Michael Powell and others, all of which have been helpful. This book fills the need in part at least and does so not only expertly but handsomely. Agaves and cacti are granted prime positions in separate sections at the beginning of the book, after which other plant families follow (monocots and dicots mixed). Each plant is superbly treated with an excellent photo, non-technical description, and indications of where in the park the plant might be found. (Eager to see Texas *Thelopody*? Follow the instructions to it and to its congener *T.wrightii*, too.) These are some of the showier plants; there are many more. By definition coverage is limited. The book does not pretend to be comprehensive. Rather it reflects one man's passion for the plants and the desire to share that passion. Need for a comprehensive guide to plants of the Park still exists, but this is one very worthwhile contribution to that end.

Among the four useful appendices are ones indicating the status of rare plants and the listing of plants by Park location.—*Joann Karges, Texas Christian University Library (retired), Fort Worth, Texas, U.S.A.*

FOLIA TAXONOMICA 7. TWO NEW SPECIES AND A NEW SECTION IN *EPISCIA* (GESNERIACEAE) FROM THE VENEZUELAN GUAYANA

Christian Feuillet

Department of Botany, MRC-166
Smithsonian Institution, P.O. Box 37012
Washington, D.C. 20013-7012, U.S.A.
feuillec@si.edu

ABSTRACT

Two new species of *Episcia* (Gesneriaceae) are described from the state of Amazonas in the Venezuelan Guayana. **Episcia duidae** sp. nov. resembles *E. reptans* in section *Episcia* by its flowers, but differs by its smaller vegetative parts and densely appressed-pubescent leaves. **Episcia rubra** sp. nov. resembles *E. fimbriata* and *E. sphalera* vegetatively, but differs by its red corollas. The latter three belong in subsection **Trematanthera** raised here to the rank of section.

RÉSUMÉ

Deux espèces d'*Episcia* (Gesneriaceae) sont décrites de l'état d'Amazonas en Guyane Vénézuélienne. **Episcia duidae** ressemble par ses fleurs à *E. reptans* dans la section *Episcia*, mais en diffère par ses organes végétatifs plus petits et les trichomes foliaires denses et appliqués. **Episcia rubra** ressemble par ses caractères végétatifs à *E. fimbriata* et *E. sphalera*, mais en diffère par ses corolles rouges. Ces trois espèces appartiennent à la sous-section **Trematanthera** élevée ici au rang de section.

RESUMEN

Se describen dos nuevas especies de *Episcia* (Gesneriaceae) del estado de Amazonas en la Guayana venezolana. **Episcia duidae** sp. nov. parece a *E. reptans* en la sección *Episcia* por sus flores, pero varía por sus partes vegetativas más pequeñas y hojas densamente aplicado-pubescentes. **Episcia rubra** sp. nov. parece a *E. fimbriata* y *E. sphalera* vegetativamente, pero varía por sus corolas rojas. Los últimos tres pertenecen a la subsección *Trematanthera*, que aquí elevamos al grado de sección.

The two new species of the subfamily Gesnerioideae Link described below were collected in the Venezuelan state of Amazonas. They belong to *Episcia* Mart. in the tribe Episcieae Endl. Since the regional treatment by Leeuwenberg (1958) and the formal infrageneric classification he proposed for *Episcia*, the genus has been split into four groups. Most authors now follow Wiehler (1973, 1978) in adopting *Alsobia* Hanst. and *Paradrymonia* Hanst., as well as the transfer of several *Episcia* species to *Nautilocalyx* Linden ex Hanst. The transfer to the other genera affected all the species of six of the seven sections and in section *Episcia*, three of the five subsections. The current concept of *Episcia* is the equivalent of two of the subsections of Leeuwenberg (1958), i.e. section *Episcia* subsections *Episcia* and *Trematanthera* Leeuwenb., and follows the most recent molecular studies (Smith 2000; Zimmer et al. 2003; Clark et al. 2006).

Episcia Mart., Nova Gen. Sp. 3:39. Jan–Jun 1829. Type: *E reptans* Mart. (Lectotype: cf. Leeuwenberg, Gesner. Guiana 309. 1958).

1.—Sect. Episcia

Anther cells dehiscing throughout by a longitudinal split.

Episcia reptans (type), *E. andina* Wiehl., *E. cupreata* (Hook.) Hanst., *E. lilacina* Hanst., *E. prancei* Wiehl., *E. xantha* Leeuwenb. & *E. duidae* sp. nov.

Episcia duidae Feuillet, sp. nov. (**Fig. 1**). Type: VENEZUELA. Amazonas. Dept. Alto Orinoco: Cerro Duida, Culebra Creek, 1500–1600 m, 21 Nov 1950 (fl), *B. Maguire, R.S. Cowan & J.J. Wurdack 29634* (holotype: US; isotype: NY).

Herba stolonibus, repens. Basis stolonum petiolique juniores trichomatibus rubris. Folia dense hirsuta praeter supra nervos medios et laterales; trichomata multicellulares, apice glandulosi. Calyx hirsutus, lobi integri, vel dentati. Corolla coccinea, tubus longe villosus.

Mat forming stoloniferous herb; whole plant with long, multicellular, gland-tipped trichomes, old stem with a few short trichomes (*Berry et al. 4972*) or 5–8 mm long, dense trichomes (*Cowan & Wurdack 31288*). Leaves

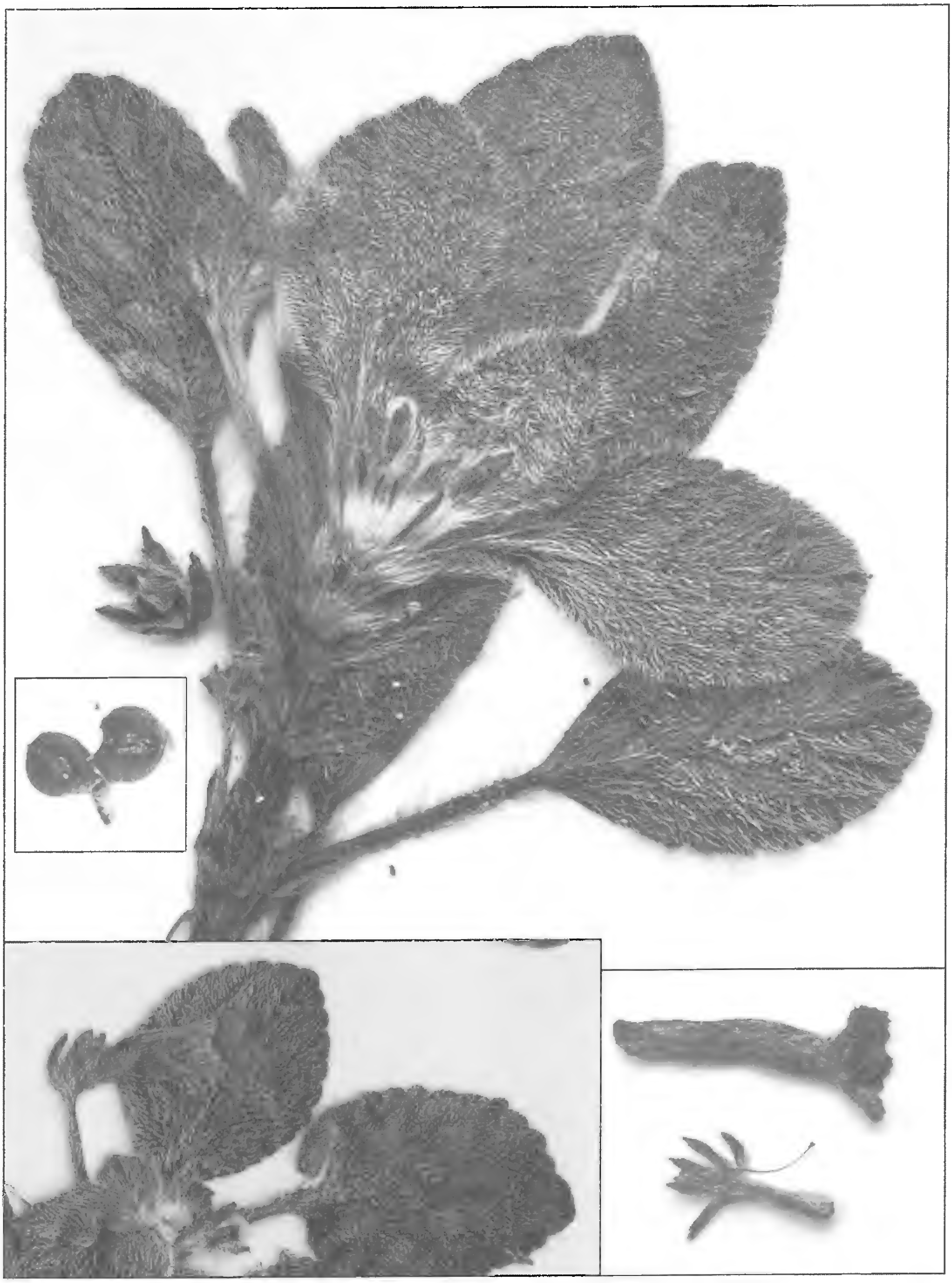

Fig. 1. *Episcia duidae* Feuillet. Plant, apex of growing stem showing young stolons (left), young leaves (low right leaf petiole 28 mm), and flower buds (middle), *Cowan & Wurdack 31288* (NY); bottom left, older flower with open corolla (total corolla length 21 mm), *Maguire et al 29634* (isotype: NY); bottom right, calyx with gynoecium and detached corolla (total corolla length 19 mm), *Berry, Huber & Rosales 4972* (US); middle left, opened capsule (left valve 4.7 mm long), *Cowan & Wurdack 31288* (NY).

opposite, equal or subequal in a pair, clearly larger in proximal part of the stem; petiole 0.5–3 cm long, hirsute, trichomes 2–2.5 mm long; blade carnose, suborbicular-ovate to broadly elliptic, 2–4.5 × 1.4–2.5 cm, base rounded to obtuse, apex rounded to broadly obtuse, margin crenate, with dense, long, appressed, yellow trichomes on both surfaces, except above on the main veins that show their dark green color, 3–5 main veins on each side of the midrib, ending in margin sinuses. Inflorescence a reduced pair-flowered cyme, fasciculate, 1–4-flowered, axillary in the apical part of the stem with small leaves still growing; pedicel about 8 mm long. Flowers with sepals free, entire or 1–2-toothed in apical half in the same flower, lanceolate to oblanceolate, 8–9 × 1.5 mm, densely hirsutulous on both sides, the posterior one slightly involute and narrower; corolla held transversal in the calyx, crimson, basal gibbosity 3 × 4 mm, uniformly densely pilose, tube 15–18 mm long, densely appressed-pubescent outside, inside papillate in apical third and glabrous below, lobes suborbicular, rounded, serrulate, 7 × 4 mm, glabrous on both sides except at very base where joining the tube; stamens inserted about 2.5 mm above base of corolla tube, filament glabrous, broadened at base, anthers suborbicular, 1.5 × 1.2–1.5 mm; dorsal glands fused in a tongue-like gland, about 1 × 1 mm; ovary superior, ovoid, 3 × 3 mm, densely sericeous–pilose, style 12 mm long, densely pilose. Capsule globose, 4.5–5 mm long.

Distribution.—*Episcia duidae* is known from Cerro Duida (Munic. Alto Orinoco) and Serranía Parú (Munic. Atures) in the state of Amazonas (Venezuela) between 1500 and 2000 m. It was collected at the bases of waterfalls and in wet crevices.

Phenology.—It has been collected in bloom in February–March and November, and in fruit in February.

Episcia duidae resembles the red-flowered species of subsection *Episcia*: *E. andina* Wiehl., *E. cupreata* (Hook.) Hanst., and *E. reptans* Mart. Inside the corolla tube, *E. duidae* has the apical third with large papillae, *E. cupreata* and *E. reptans* have a ring of glandular trichomes in the throat, *E. andina* is said to have a corolla glabrous inside (Wiehler 1984; but this could not be checked). The style is densely pilose in *E. duidae*, unknown in *E. andina*, and glabrous in the other two, occasionally with scattered trichomes at the apex in *E. cupreata*. *Episcia duidae* and *E. andina* differ from the other two by much smaller leaf blades with a long dense appressed pubescence on both sides rather than hirsute leaf blades found in the other two species. The corolla of *E. reptans* is about twice as long as in the other three; it is cylindric and nearly straight in *E. duidae* and *E. reptans*, infundibuliform and straight in *E. andina*, and clearly curved in the middle in *E. cupreata*. *E. duidae* differs from *E. cupreata* by the dense appressed (versus hirsute) indumentum on the leaf blades, the corolla posture transverse (versus oblique) in the calyx, with a tube straight (versus curved near middle), densely appressed-pubescent (versus pilose), smaller corolla lobes, and a style densely pilose (versus glabrous or with a few trichomes near the apex). *Episcia duidae* was "sp. B" in Feuillet and Steyermark (1999), where it should be noted that numbers 2 and 3 were switched in the first bracket of the "Key to the species of *Episcia*" in that publication.

Etymology.—The new species is named after Mt. Duida at the base of which the type specimens have been collected.

Paratypes: **VENEZUELA. Amazonas. Dept. Atures:** Serranía Parú, 2000 m, 7 Feb 1951, *R.S. Cowan & J.J. Wurdack 31288* (NY), 1200–1250 m, 5–7 Mar 1991, *P.E. Berry, O. Huber & J. Rosales 4972* (MO, US).

2.—Sect. Trematanthera (Leeuwenb.) Feuillet, sect. nov. Basionym: *Episcia* subsect. *trematanthera* Leeuwenb., Blumea 7:309–310. 1958.

Anther cells dehiscing only on the basal half by a partial split.
Episcia sphalera Leeuwenb. (type), *E. fimbriata* Fritsch & *E. rubra* sp. nov.

Episcia rubra Feuillet, sp. nov. (**Fig. 2**). Type: VENEZUELA. Amazonas. Dept. Atures: Río Coro-Coro, W of Serranía de Yutajé, 3 km N of settlement of Yutajé, along a small tributary, 5°38'N, 66°07'W, 200 m, 19 Feb 1987, *B.K. Holst & R.L. Liesner 3087* (holotype: US-3120092; isotypes: MO, US-3284218).

Herba stolonibus; caules repentes, dense hirsuti; lamina foliorum bullata, hirsuta; calyx hirsutus; corolla coccinea.

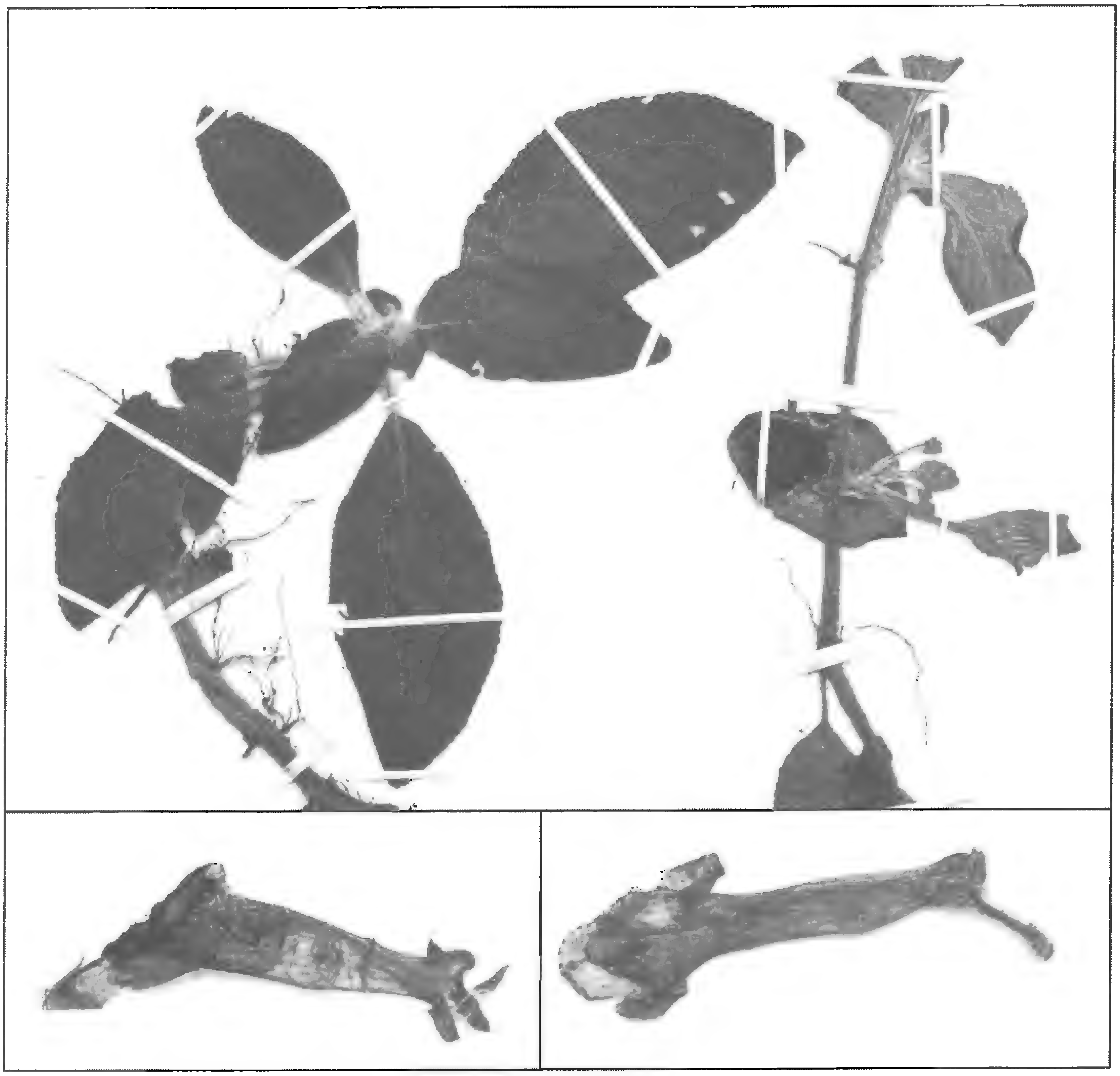

Fig. 2. ***Episcia rubra*** **Feuillet. Plant: top (low middle leaf blade 83 mm long),** ***Holst & Liesner 3087*** **(holotype: US). Flower bottom left (total corolla length 21 mm),** ***id.*** **(isotype: US), bottom right (total corolla length 25 mm),** ***id.*** **(isotype: MO).**

Herb terrestrial, creeping with short stolons; stem with long, multicellular, fuzzy, dense, yellowish trichomes. Leaves opposite, equal or subequal in a pair, clearly larger in proximal part of the stem; petiole 0.5–2.5 cm long, trichomes longer than on the stem; blade 2.5–9 × 1.5–4.5 cm, ovate to elliptic, base acute to obtuse, apex obtuse, margin crenate, ciliate with a tuft of trichomes at apex of each tooth, above pebbled, with trichomes at apex of each of the bullae, beneath with dense, long, silvery indumentum, 6–9 main veins on each side of the midrib. Inflorescence a reduced pair-flowered cyme, fasciculate, 1–4-flowered, axillary in the apical part of the stem with small leaves still growing; pedicels 8–1.5 mm long, hirsute, with long, fuzzy, dense, yellowish trichomes. Flower: sepals free, oblanceolate, 2–3.5 × 1 mm, apex acute, tip and 1–2 teeth thickened, hirsute, trichomes 1.8–2.3 mm long, fuzzy, dense, yellowish; corolla oblique in the calyx, crimson, basal gibbosity 1.5–2 mm long, conical, rounded distally, tube 1.2–1.6 cm long, outside with scattered, 1 mm long trichomes, lobes suborbicular, 3 × 4 mm, serrulate; stamens inserted 2–3 mm from the base of the tube, filaments 9–12 mm long, anthers reniform, about 1 × 1 mm, cells divergent, dehiscence wide at base, narrow then absent toward apex; nectary comprised of one dorsal tongue-shaped gland, 0.8

× 0.5 mm; ovary superior, ovoid, 2.5 × 1.5 mm, hirsute, trichomes 1.5–2 mm long, style 15 mm long, glabrous, stigma papillose. Young fruit subspherical, 3.5 mm in diameter, hirsute with yellowish trichomes, 1–1.5 mm long.

Distribution and phenology.—*Episcia rubra* is known only from the type collection from crevices in moist, shaded, rocky canyon along a tributary of Río Coro-Coro, in Amazonas, Venezuela, around 200 m in elevation. It was blooming and had young fruits in February.

The anthers dehiscent only in the basal half place *Episcia rubra* in sect. *Trematanthera* with *E. fimbriata* Fritsch and *E. sphalera* Leeuwenb. among which it differs by its red corollas.

Etymology.—The new species is named after the color of its red corolla, unique in *Episcia* sect. *Trematanthera.*

KEY TO THE SPECIES OF *EPISCIA* FROM THE GUIANA SHIELD

1. Corolla red or red-orange.
  2. Petiole of mature leaves 30–70 mm long; corolla 20–35 mm long.
    3. Corolla tube cylindric, 3–3.5 cm long, nearly straight, pinkish in the throat, all 5 lobes spreading. Colombia, Venezuela (western and Amazonas, Bolivar), French Guiana, Guyana, Surinam, Brazil (Minas Gerais and northern), Peru ____ **E. reptans**
    3. Corolla tube ampliate to twice as wide at throat than at base, ≤ 2.5 cm long, and suddenly curved at middle, yellow in the throat, 2 dorsal lobes recurved. Central America, Colombia, Venezuela (western), Brazil (Amapá), Ecuador, Peru + Guianas (cultivated, sometimes escaped) ____ **E. cupreata**
  2. Petiole of mature leaves 10–30 mm long; corolla tube 12–18 mm long.
    3. Calyx lobes 7–8 mm long; corolla tube densely appressed-pubescent; anther cells opening by a longtudinal slit from base to apex. Venezuela (Amazonas) ____ **E. duidae**
    3. Calyx lobes 2–3 mm long; corolla tube sparsely hirsute; anther cells dehiscing only on their basal half. Venezuela (Amazonas) ____ **E. rubra**
1. Corolla yellow, white, or lavender to light blue.
  4. Corolla yellow; calyx lobes obovate. Venezuela (Amazonas), Guyana, Surinam, French Guiana ____ **E. xantha**
  4. Corolla tube white, lobes white or lavender; calyx lobes lanceolate or spathulate.
    5. Corolla lobes white; leaf blades pale green; calyx lobes lanceolate. Brazil (Amapá, Pará), Surinam, French Guiana ____ **E. sphalera**
    5. Corolla with lavender markings or lobes lavender to blue; leaf blades variously colored; calyx lobes lanceolate or spathulate.
      6. Corolla white with lobes lavender to blue; calyx lobes spathulate; leaf blades mostly with color markings; anther cells opening by a longitudinal slit from base to apex. Central America, Colombia + Guianas (cultivated, rarely escaped) ____ **E. lilacina**
      6. Corolla white, sometimes with lavender markings; calyx lobes lanceolate; leaf blades mostly green, sometimes margin red beneath; anther cells dehiscing only on their basal half. Colombia, Venezuela (Amazonas), Brazil (western and northern), Peru ____ **E. fimbriata**

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FOLIA TAXONOMICA 8. *PASSIFLORA TECTA* (PASSIFLORACEAE), A NEW SPECIES IN SUBGENUS *PASSIFLORA* FROM THE GUIANAS

Christian Feuillet

Department of Botany, MRC-166
Smithsonian Institution, P.O. Box 37012
Washington, D.C. 20013-7012, U.S.A.
feuillec@si.edu

ABSTRACT

Passiflora tecta, a new species with red flowers, is described from Guyana. It belongs in subgenus *Passiflora* supersection *Coccinea* and resembles *Passiflora coccinea* and *P. miniata*. The three species can easily be distinguished using corona characters. The outer corona filaments of *P. tecta* are scarlet and held nearly erect, slightly oblique inward like a narrow cone around the androgynophore. In *P. coccinea* the outer corona filaments are white and held oblique inward, while in *P. miniata* they are dark purple and nearly erect, slightly oblique outward like the rim of a flower pot.

RÉSUMÉ

Passiflora tecta, espèce nouvelle à fleurs rouges, est décrite de Guyana. Elle appartient au sous-genre *Passiflora* supersection *Coccinea* et est proche de *Passiflora coccinea* et *P. miniata*. Ces trois espèces sont faciles à reconnaître par les caractères de la couronne. Les filaments externes de *P. tecta* sont rouges et dressés, légèrement obliques en cône étroit autour de l'androgynophore. Les filaments externes de *P. coccinea* sont blancs et obliques en cône, tandis que ceux de *P. miniata* sont violet foncé et dressés, légèrement obliques vers l'extérieur comme le rebord d'un pot de fleur.

In Feuillet (2007) two new species were described in *Passiflora* subg. *Passiflora* supersect. *Coccinea* Feuillet & J.M. MacDougal, and a key to the species was given. In that paper, one branch in bracket 11 of the key led to "**P. sp.** (Guyana)", known only from photographs. Since publication of that manuscript, herbarium material has become available, thus allowing a good description to be drawn from actual specimens. This new species is described as *Passiflora tecta*.

Passiflora tecta Feuillet, sp. nov. (**Fig. 1–2**). Type: GUYANA. Potaro–Siparuni: Eagle Mountain, around the OMI base camp, 5°15'18"N, 59°6'59"W, 383 m, fl., 10 Sep 2006, *K.M. Redden 4132* (holotype: US; isotypes: BRG, K).

Passiflora tecta in subg. *Passiflora* supersect. *Coccinea* pertinens; corona triseriata; *P. coccineae* affinis, coronae filamentis extimis rubris differt; *P. miniatae* affinis, coronae filamentis extimis rubris versus atropurpureis, intime versus extrinsecus obliquis differt.

Liana climbing on shrubs and small trees at forest edge, probably reaching the canopy. Young stems terete, slightly striate, with short, irregularly curved trichomes. Tendrils long, thin, with short arched trichomes. Vegetative bud in apical position, less than 1 mm away from the rest of the axillary complex (petiole, stipules, pedicel, tendril), prophylls acuminate at apex, densely short-pubescent. Stipules linear, 2.5 × 0.8 mm, short-pubescent, deciduous before the leaf differentiate in petiole and blade, leaving a round scar. Petiole 8–12 mm long, curved at base, with 2 lateral glands at the very base; glands scar-like, glandular surface oval, ca. 1 × 1.5 mm, with 1–2 tufts of long white trichomes, otherwise glabrous, rim minute pubescent. Blade ovate, 5–10 × 2.5–6 cm, bi-serrate, teeth ending in small, stipitate, round glands, acuminate and mucronate at the apex, broadly cordate and briefly cuneate at the base, drying brown adaxially and yellow-brown abaxially, 2–3 main lateral veins on each side of the midrib, the first pair about 2/3 as long as the midrib, tertiary venation scalariform. Inflorescence sessile, 1-flowered. Pedicels erect, 4.5–6.5 cm long, with dense short pubescence. Bracts three, verticillate, orange red, ovate, concave, 3–5 × 2–2.5 cm, free to base, round at the apex, glandular serrate at the margin on the apical two-thirds, with dense short trichomes on both surfaces. Flowers orange red, perianth lobes adaxially whitish at base; hypanthium 7 mm long, 9 mm broad on live material, round at base, inflated with the point of contact with the pedicel invaginated,

Fig. 1. *Passiflora tecta* in Guyana in Feb 2007 (photo by C. Kelloff). Petal 2.3 cm long.

Fig. 2. *Passiflora tecta* in Guyana in Feb 1990 (photo by C. Feuillet). Androgynophore 1.7 cm long.

Fig. 3. *Passiflora coccinea* in French Guiana in April 1985 (*Feuillet 2128*; photo by C. Feuillet). Outer corona filaments ca. 1 cm long.

Fig. 4. *Passiflora miniata* in cultivation in March 1990 (photo by C. Feuillet). Outer corona filaments 2.2 cm long.

densely short pubescent outside; sepals narrow-oblong, 2–2.5 cm long, plus a subapical awn, 0.7–1.0 cm long, 0.5–0.6 cm broad, short-pubescent in the parts exposed in bud, otherwise glabrous; petals similar to the sepal, slightly narrower, thinner, not awned, glabrous; corona bright red, in 3 rows, filamentose, the first 2 rows composed of laterally compressed, narrowly triangular filaments, erect to 70–80°, slightly oblique, leaning against the androgynophore and the ovary, the first row about 12 mm long, the second row about 9 mm long, the third row filiform, about 5–6 mm long; operculum borne at the top of the hypanthium, membranous, dependent to 2/3 down the hypanthium, then recurved inward, laciniate at the margin, 9–10 mm long, glabrous; nectar disc annular at the bottom of the hypanthium; limen membranous, surrounding the base of the androgynophore, 1–2 mm long, glabrous; androgynophore red throughout, cylindric, ca. 1.7 cm long, glabrous; stamen glabrous, filaments flat, pale green with red dots throughout, 6 × 1 mm, joined in a short membrane at base, anthers dorsifixed, rectangular, 6 × 2.5 mm; gynophore shorter than and covered by the membrane at the base of the androecium; ovary green, 6 mm long, 2–2.5 mm in diam., ellipsoid, densely short-pubescent; styles pink with red dots, 9–12 mm long, minutely pubescent; stigmatic surface light green, papillate. Immature fruit (according to photograph) green, hanging on elongated pedicel, hidden by yellowish green bracts.

Distribution.—The only specimen of *Passiflora tecta* known to me was collected in flower from Guyana, in the Potaro-Siparuni region, near Eagle Mountain in a clearing at the edge of the forest in September 2006. The same species has been photographed twice in Guyana, once in February 1990 (C. Feuillet) in the Upper Takutu-Upper Essequibo region near Surama, at the forest edge along a dirt road (with bud and young fruit), and again in February 2007 (C. Kelloff) in the Potaro-Siparuni region, in Kaieteur National Park (flower), though no herbarium specimens were made. The three localities are in western central Guyana and the plants were collected or photographed at the edge of lowland rainforest (less than 500 m elevation). *Passiflora tecta* could be easily confused with *P. coccinea*, the most common species of *Passiflora* in the Guianas.

Passiflora tecta sp. nov. clearly belongs to *P.* subgen. *Passiflora* supersect. *Coccinea* due to its distinctive leaves with serrate margins, red floral bracts with glandular-serrate margins, red-colored perianth, and straight corona filaments that form a cone angled towards the androgynophore. In this supersection, *P. tecta* most closely resembles *P. coccinea* Aubl. (Fig. 3), a species with a large Amazonian and Guianan distribution described from French Guiana (Aublet 1775). However, the Guianan endemic *P. tecta* has narrow-elliptic rather than ovate bracts and red rather than white outer corona filaments. *Passiflora tecta* also resembles *P. miniata* Vanderplank (Fig. 4), described from western Amazonia (Colombia, Brazil, Peru, and Bolivia) by John Vanderplank (2006), from which it differs in its outer corona filaments that are orange-red and slightly oblique inwards, rather than dark purple and slightly oblique outwards.

Etymology.—The Latin specific epithet means "covered." This refers to the three rows of corona filaments that restrict pollinator access to the nectar chamber contrary to the condition in *P. miniata*, where only the innermost row of filaments guard the throat.

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BOOK REVIEW

James H. Everitt, Robert I. Lonard, and Christopher R. Little. 2007. **Weeds in South Texas and Northern Mexico: A Guide to Identification.** (ISBN 978-089672-614-7, pbk.). Texas Tech University Press, Box 41037, Lubbock, Texas 79409-1037, U.S.A. (**Orders:** www.ttup.ttu.edu, ttup@ttu.edu, 1-806-742-2892; 1-806-742-2979 fax). $19.95, 222 pp., 6" × 9".

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Any book on weeds must perfunctorily start with a definition of "weed," and this one does that, encompassing the usual criteria. In fact, of course, a number of these weeds are wildflowers cherished or at least respected by native plant enthusiasts: *Cirsium texana, Pluchea purpurascens, Oenothera speciosa* and others. The text hints at reasons for such plants to be so designated though not establishing full justification. After the one fern (*Salvinia molesta*), the text arrangement is by family, dicots and monocots mixed, each species with a color photograph and apt description—except that there is no indication of plant dimensions, size of flower or leaf, or the height to which the plant normally grows. Despite this deficit, the guide will be quite helpful. Perhaps most useful is the section on Poaceae, the majority of which are pervasive throughout the state and adjacent areas.

The excellent photographs and superior descriptions for some of these confusing species are more than adequate even for a beginning amateur. Appendices name pathogens (viral and fungal), nematodes, and insect pests of some of the plants that particularly need to be controlled in lawn and garden care as well as for agricultural management. This little guide has useful relevance throughout the state of Texas and adjacent areas.—*Joann Karges, Texas Christian University Library (retired), Fort Worth, Texas, U.S.A.*

A SYNOPSIS OF *PACHYPHYLLUM* (ORCHIDACEAE)

Eric A. Christenson

4503 21st Ave. West
Bradenton, Florida 34209, U.S.A.
orchideric@juno.com

ABSTRACT

The 41 accepted species of the neotropical orchid genus *Pachyphyllum* Kunth are enumerated. Types are cited for all names including 10 new lectotypifications. The genus is divided into 3 sections, one based on the genus *Orchidotypus* Kraenzl. and one wholly new, **P.** sect. **Capitulum** E.A. Christ. Three names are considered synonyms within *Pachyphyllum* and eight names are excluded from the genus.

Key Words: *Pachyphyllum*, Orchidaceae, Neotropics

RESUMEN

Se enumeran las 41 especies aceptadas del género de orquídeas neotropical *Pachyphyllum* Kunth. Se citan los tipos de todos los nombres incluyendo 10 nuevas lectotipificaciones. El género se divide en 3 secciones, una basada en el género *Orchidotypus* Kraenzl. y otra totalmente nueva, ***P.*** sect. ***Capitulum*** E.A. Christ. Tres nombres se consideran sinónimos en Pachyphyllum y ocho nombres se excluyen del género.

Despite the characteristic growth habit and relative abundance of available herbarium material, the genus *Pachyphyllum* remains woefully understudied. Concentrated biodiversity studies in the Department of Cusco in southern Peru (www.andesamazon.org) have recorded many species in the genus, some new to Peru and some, no doubt, new to science. Critical study and dissemination of this information has just begun (Repasky & Christenson, in press).

Recent collections of *Pachyphyllum ecallosum* from the Department of Cusco, Peru, have emphasized the distinct nature of its inflorescence. Unlike the few flowered inflorescences of the type collection from the Department of Huancavelica, more recent collections consistently bear 4–6 flowers arranged in a well defined capitulum. A new section is proposed for *P. ecallosum* and its sister species, *P. tortuosum*. In addition, the genus *Orchidotypus* is given formal status as a section of *Pachyphyllum*.

KEY TO THE SECTIONS

1. Flowers arranged in a dense capitulum ______ **P.** sect. **Capitulum**
1. Flowers arranged in a raceme.
   2. Sepals and petals fused together at the base forming a tube for half their length ______ **P.** sect. **Orchidotypus**
   2. Sepals and petals free ______ **P.** sect. **Pachyphyllum**

Pachyphyllum section **Pachyphyllum.** Type species: *Pachyphyllum distichum* Kunth.

Pachyphyllum breviconnatum Schltr., Repert. Spec. Nov. Regni Veg. Beih. 9:115. 1921; Repert. Spec. Nov. Regni Veg. Beih. 57: t. 130, nr. 510. 1929. Type: PERU. Dept. Cusco: Prov. Paucartambo, below Tres Cruces Inn, 3600–3700 m, *Weberbauer* 6976 (holotype: B, destroyed; lectotype, designated here: US; isolectotypes: F, MOL).

Comment.—The US specimen is designated lectotype as there are better flowers available than on either of the two sheets at F or the two sheets at MOL.

Pachyphyllum bucarasicae Kraenzl., Pflanzenr. 4, 50:25. 1923. Type: COLOMBIA. Dept. Santander: Bucasasica, 3300 m, *Kalbreyer* 918 (holotype: ?W).

Pachyphyllum capitatum Kraenzl., Bot. Jahrb. Syst. 37:386. 1906. Type: PERU. Dept. Amazonas: E of Chachapoyas, between Tambo Ventillas and Piscohuañuna, 2600–2700 m, *Weberbauer* 4421 (holotype: B, destroyed; lectotype, designated by Bennett & Christenson in Icon. Orchid. Peruv. pl. 739, 2001: MOL).

Pachyphyllum cardenasii Smith & Harris, Contr. Gray Herb. 114:12. 1936. Type: BOLIVIA. Dept. Cochabamba: Prov. Ayopapa, Sailapata, 3000 m, *Cardenas* 3289 (lectotype, designated here: AMES; isolectotype: G).

Comment.—No holotype was designated in the protologue.

Pachyphyllum costaricense (Ames & C. Schweinf.) L.O. Wms., Lilloa 3:481. 1938. *Centropetalum costaricense* Ames & C. Schweinf., Sched. Orch. 10:110. 1930. Type: COSTA RICA. Prov. San José: near Finca La Cima, above Los Lotes, N of El Copey, 2100–2400 m, 21–22 Dec 1935, *Standley* 42600 (holotype: AMES; isotype: US).

Pachyphyllum crystallinum Lindl., Orch. Linden. 18. 1846. Type: VENEZUELA: Merida, 10,000 ft, *J. Linden* 686 (holotype: K).

Pachyphyllum cuencae Rchb.f., Linnaea 41:31. 1877. Type: ECUADOR: Surucucho near Cuenca, 2900 m, Jul 1864, *Jameson s.n.* (holotype: W, isotype: AMES).

Pachyphyllum cyrtophyllum Schltr., Repert. Spec. Nov. Regni Veg. 15:217. 1918, in textu; Repert. Spec. Nov. Regni Veg. Beih. 10:80. 1922. Basionym: *Pachyphyllum falcifolium* Schltr., Repert. Spec. Nov. Regni Veg. 10:460. 1912, non Rchb.f. Type: BOLIVIA: in moss, near Ingenio, *R.S. Williams* 1631 (holotype: B, destroyed; lectotype, designated here: NY; isolectotype: BM).

Comment.—The NY specimen is here designated lectotype. *Pachyphyllum confusum* Kraenzl. is a new name based on Schlechter's *P. falcifolium*, but was published after Schlechter himself had published his own new name.

Pachyphyllum confusum Kraenzl., Pflanzenr. 4, 50:22. 1923.

Pachyphyllum dalstroemii Dods., Orquideología 20(3):278. 1997. Type: ECUADOR: Loja, San Pedro road from Loja to Vilcabamba, 2500 m, Apr 1984, *Dalström & Hoijer* 802 (holotype: SEL).

Pachyphyllum denticulatum (Ruiz & Pav.) Schltr., Repert. Spec. Nov. Regni Veg. Beih. 9:180. 1921. *Fernandezia denticulata* Ruiz & Pav., Syst. Veg. Fl. Peruv. & Chil. 1:240. 1798. Type: PERU. Dept. Huanuco: Pillao, *Pavon s.n.* (holotype: MA).

Pachyphyllum distichum Kunth, Nov. Gen. & Sp. 1:339. 1816. Type: ECUADOR: Loxa, Gonzanam, 6420 ft (1070 hexap.), *Humboldt & Bonpland s.n.* (holotype: P).

Pachyphyllum falcifolium Rchbf., Linnaea 41:32. 1877. Type: ECUADOR: Loja, Sep, *Jameson s.n.* (holotype: W; isotype: AMES).

Pachyphyllum favosifolium Kraenzl., Pflanzenr. 4, 50:23. 1923. Type: COLOMBIA. Dept. Antioquia: Sonson, 3300 m, *Kalbreyer* 1935 (holotype: ?W).

Pachyphyllum hagsateri Dods., Orquideología 20:104. 1996. Type: ECUADOR. Sucumbios, El Mirador between Playón and San Gabriel, 3300 m, 8 Jul 1990, *Dodson et al.* 18501 (holotype: RPSC; isotypes: MO, QCNE).

Pachyphyllum hartwegii Rchb.f., Bonplandia 2:219. 1854. *Pachyphyllum distichum* Lindl. ex Rchb.f., Bonplandia 3:219. 1855, non Kunth. Type: ECUADOR: Pichincha, *Hartweg s.n.* (holotype: W).

Pachyphyllum herzogii Schltr., Meded. Rijks-Herb. Leiden 29:80. 1916. Type: BOLIVIA: Comarapa, 2600 m, Apr 1911, *Herzog* 1946 (holotype: L; isotype: Z).

Pachyphyllum lycopodioides Schltr., Repert Spec. Nov. Regni Veg. Beih. 9:116. 1921; Repert. Spec. Nov. Regni Veg. Beih. 57: t. 130, nr. 511. 1929. Type: PERU: Huanuco, SW of Monzón, 3400–3500 m, *Weberbauer* 3327 (holotype: B, destroyed; lectotype, designated here: MOL).

Pachyphyllum micrangis Schltr., Repert. Spec. Nov. Regni Veg. Beih. 7:203. 1920; Repert. Spec. Nov. Regni Veg. Beih. 57: t. 73, nr. 281. 1929. Type: COLOMBIA: Cauca, ca. 3000 m, *M. Madero s.n.* (holotype: B, destroyed, drawings AMES; lectotype, designated here: t. 73, nr. 281, loc. cit.).

Comment.—The published type drawing is designated as the lectotype, noting the augmentation of the unpublished drawings at AMES. No duplicates of Madero's collections are known to be extant.

Pachyphyllum micranthum Schltr., Repert. Spec. Nov. Regni Veg. Beih. 7:204. 1920; Repert. Spec. Nov. Regni Veg. Beih. 57: t. 63, nr. 282. 1929. Type: COLOMBIA: Cauca, *M. Madero s.n.* (holotype: B, destroyed, drawings AMES; lectotype, designated here: t. 73, nr. 282, loc. cit.).

Comment.—The published type drawing is designated as the lectotype, noting the augmentation of the unpublished drawings at AMES. No duplicates of Madero's collections are known to be extant.

Pachyphyllum minus Schltr., Repert. Spec. Nov. Regni Veg. 10:460. 1912; Repert. Spec. Nov. Regni Veg. Beih. 58: t. 60, nr. 239. 1930. TYPE: BOLIVIA: Unduavi, ca. 3200 m, Nov. 1910, *O. Buchtien s.n.* (HOLOTYPE: B, destroyed; LECTOTYPE, designated here: t. 60, nr. 239, loc. cit.).

Pachyphyllum nubivagum L.O. Wms., Lilloa 3:483. 1938. TYPE: COLOMBIA. DEPT. SANTANDER: western slope of Páramo de las Puentes, above La Baja, 3300–3400 m, 25–31 Jan 1927, *Killip & Smith* 18161 (HOLOTYPE: AMES).

Pachyphyllum parvifolium Lindl. in Hook., Ic. Pl. 2: t. 117. 1837. TYPE: PERU. DEPT. AMAZONAS: Chachapoyas. 1836, *Mathews s.n.* (HOLOTYPE: K).

Pachyphyllum pastii Rchb.f., Bonplandia 3:239. 1855. TYPE: ECUADOR: Quito, *Jameson* 439 (HOLOTYPE: W; ISOTYPE: K).

Pachyphyllum pectinatum Rchb.f., Xenia Orchid. 3:22. 1881. TYPE: BOLIVIA. PROV. LARECAJA: Sorata, 3100–3200 m, May 1860, *Mandon* 1152 *p.p.* (HOLOTYPE: W; ISOTYPES: MICH, NY).

Pachyphyllum peperomioides Kraenzl., Pflanzenr. 4, 50:27. 1923. TYPE: COLOMBIA. PROV. NARIÑO: Pasto, 3300 m, Jun 1878, *F.C. Lehmann s.n.* (HOLOTYPE: W).

Pachyphyllum piesiki Szlachetko, Mytnik-Ejsmont & Rutkowski, Orchidee (Hamburg) 58:94. 2007. TYPE: ECUADOR: PROV. CHINCHIPE: near Yangana, Nov 2005, *Szlachetko et al. s.n.* (HOLOTYPE: UGDA-DLSz).

Pachyphyllum pseudodichaea Rchb.f., Xenia Orchid. 3:22. 1878. TYPE: BOLIVIA. PROV. LARECAJA: Sorata, 3100–3200 m, May 1860, *Mandon* 1152 *p.p.* (HOLOTYPE: W; ISOTYPE: NY).

Pachyphyllum serra Rchb.f., Bonplandia 3:219. 1855. TYPE: PERU. DEPT. AMAZONAS: Chachapoyas, *Mathews s.n.* (HOLOTYPE: W).

Pachyphyllum squarrosum Lindl., Ann. & Mag. Nat. Hist. 15:107. 1845. TYPE: COLOMBIA. PROV. POPAYÁN: 10,500 ft, *leg.* ? 1409 (HOLOTYPE: K; ISOTYPE: K).

Pachyphyllum stuebelii Schltr., Repert. Spec. Nov. Regni Veg. Beih. 7:204. 1920; Repert. Spec. Nov. Regni Veg. Beih. 57: t. 73, nr. 283. 1929. TYPE: COLOMBIA: Tolima, Volcan de Tolima, above 4000 m, Nov 1868, *A. Stübel* 213 (HOLOTYPE: B, destroyed, drawing AMES; LECTOTYPE, designated here: t. 73, nr. 283, loc. cit.).

Comment.—No duplicates of Stübel's collections are known to be extant. The published type drawing is designated as the lectotype.

Pachyphyllum tajacayaense D.E. Benn. & E.A. Christ., Icon. Orchid. Peruv. pl. 739. 2001. TYPE: PERU. DEPT. HUANCAVELICA: Tayacaja, Dist. Huacocolpa, zone Inquilapata, 2900 m, *M. León M. ex Bennett* 7877 (HOLOTYPE: MOL).

Pachyphyllum sect. **Orchidotypum** (Kraenzl.) E.A. Christ., **stat. nov.** BASIONYM: *Orchidotypus* Kraenzl., Bot. Jahrb. Syst., 37:383. 1906. TYPE SPECIES: *Orchidotypus muscoides* Kraenzl.

The genus *Orchidotypus* has been considered a synonym of *Pachyphyllum* with the notable exceptions of Senghas (1995) and Szlachetko et al. (2007). The fusion of the sepals and petals into a tube, however, appears to be ample reason to maintain them as a section of *Pachyphyllum*. Species of this section are also consistently smaller statured than species of section *Pachyphyllum*.

Pachyphyllum aurorae D.E. Benn. & E.A. Christ., Icon. Orchid. Peruv. pl. 546. 1998. TYPE: PERU: Chanchamayo, 2700 m, 12 Apr 1996, *O. del Castillo ex Bennett* 7501 (LECTOTYPE, designated here: MOL; ISOLECTOTYPE: NY).

Comment.—Bennett and Christenson (1998) neglected to designate the holotype in the original publication. The name is lectotypified with the specimen at MOL (transferred from USM).

Pachyphyllum bryophytum Schltr., Repert. Spec. Nov. Regni Veg. Beih. 27:181. 1924. *Orchidotypus bryophytus* (Schltr.) Senghas, Die Orchideen, ed. 3, I/B(31):1923. 1995. TYPE: COLOMBIA. DEPT. CUNDINAMARCA: near Bogota, 2500 m, 1921, *H. Hopf s.n.* (HOLOTYPE: B, destroyed).

Comment.—No duplicates of Hopf's collections are known to be extant. Since I have nothing to go on except the original description, I think it is best to not lectotypify the name at this time. A more detailed study of the genus in Colombia is needed.

Pachyphyllum gracillimum C. Schweinf., Amer. Orchid Soc. Bull. 16:564. 1947. *Orchidotypus gracillimus* (C. Schweinf.) Senghas, Die Orchideen, ed. 3, I/B(31):1923. 1995. Type: PERU. Dept. Cusco: Prov. Urubamba, Puyupata-Tuncapata, 3200 m, 6 Aug 1942, *C. Vargas* 2932 (holotype: CUZ)

Pachyphyllum hispidulum (Rchb.f.) Garay & Dunsterv., Venez. Orch. Ill. 3:236. 1965. *Aeranthus hispidulus* Rchb.f., Linnaea 41:31. 1876; *Campylocentrum hispidulum* (Rchb.f.) Rolfe, Orchid Review 11:246. 1903; *Orchidotypus hispidulus* (Rchb.f.) Senghas, Die Orchideen, ed. 3, I/B(31):1923. 1995. Type: COLOMBIA: Santa Martha, *Purdie s.n.* (holotype: W).

Pachyphyllum muscoides (Kraenzl.) Schltr., Repert. Spec. Nov. Regni Veg. 15:216. 1918; *Orchidotypus muscoides* Kraenzl., Bot. Jahrb. Syst. 37:383. 1906. Type: PERU. Dept. Cajamarca: Prov. Chota, west of Huambos, 2700–3000 m, *Weberbauer* 4189 (B, destroyed).

Pachyphyllum microscopicum (Kraenzl.) Schltr., Repert. Sp. Nov. Regni Veg. Beih. 19:72. 1923; *Dichaea microscopica* Kraenzl., Pflanzenr. 4(50), 83:36. 1923. Type: ECUADOR: near Cuenca, ca. 3500 m, 16 Aug 1878, *F. C. Lehmann s.n.* (holotype: W).

Orchidotypus vareschii Foldats, Acta Biol. Venez. 2(4):28. 1957. Type: VENEZUELA: Edo. Trujillo, Pmo. El Púlpito, 3200 m, *Vareschi* 4527-A (holotype: VEN).

Pachyphyllum mexicanum Dressler & Hágsater, Orquidea(Mex.) 6(3):73. 1976. *Orchidotypus mexicanus* (Dressler & Hágsater) Senghas, Die Orchideen, ed. 3, I/B(31):1923. 1995. Type: MEXICO. Guerrero: Puerto El Asoleadero, entre Carrizal de Bravos y Cruz de Ocote, 2600 m, *Hágsater 2839* (holotype: MEXU; isotypes: AMES, ENCB, K, MO, SEL).

Pachyphyllum schultesii L.O. Wms., Caldasia 1(3):15. 1941. *Orchidotypus schultesii* (L.O. Wms.) Senghas, Die Orchideen, ed. 3, I/B(31):1923. 1995. Type: COLOMBIA: Páramo de Chipaque, SE of Bogota, 3200 m, 25 Sep 1941, *R.E. Schultes* 1020 (holotype: AMES).

Pachyphyllum tenue Schltr., Repert. Spec. Nov. Regni Veg. Beih. 9:116. 1921; Repert. Spec. Nov. Regni Veg. Beih. 57: t. 131, nr. 512. 1929. *Orchidotypus tenuis* (Schltr.) Senghas, Die Orchideen, ed. 3, I/B(31):1923. 1995. Type: PERU. Dept. Junin: Chanchamayo Valley, *Koehler s.n.* (holotype: B, destroyed; lectotype, designated here: t. 131, nr. 512, loc. cit.).

Pachyphyllum vaginatum Schltr., Repert. Spec. Nov. Regni Veg. Beih. 27:182. 1924. *Orchidotypus vaginatus* (Schltr.) Senghas, Die Orchideen, ed. 3, I/B(31):1923. 1995. Type: COLOMBIA: Cundinamarca, near Bogota, 2500 m, 1921, *H. Hopf s.n.* (holotype: B, destroyed).

Comment.—No duplicates of Hopf's collections are known to be extant. Since I have nothing to go on except the original description, I think it is best to not lectotypify the name at this time. A more detailed study of the genus in Colombia is needed.

Pachyphyllum sect. **Capitulum** E.A. Christ., **sect. nov.** Type species: *P. ecallosum* D.E. Benn. & E.A. Christ.

Flores in capitulum.

Pachyphyllum ecallosum D.E. Benn. & E.A. Christ., Icon. Orchid. Peruv. pl. 738. 2001. Type: PERU: Dept. Huancavelica, Tayacaja, Dist. Huachocolpa, Capcasoro, 3400 m, 15 Jun 1999, *M. León M.* 3067 (holotype: MOL).

Pachyphyllum tortuosum Foldats, Soc. Venez. Cienc. Nat. 28:115. 1969. Type: VENEZUELA. Edo Tachira: Rio Quinimari, Quebrada Las Copas, 2600–2630 m, *G. C. K. Dunsterville & E. Dunsterville* 90 (holotype: VEN; isotype: K).

The recent collection of *P. tortuosum* from southern Peru (Dept. Cusco, Machu Picchu, Wiñay Wayna, *Nauray* 181, CUZ) strengthens the relationship of these two species.

EXCLUDED SPECIES

Pachyphyllum echinocarpon (Sw.) Spreng., Syst. Veg. 3:731. 1826. *Epidendrum echinocarpon* Sw., Prodr. 124. 1788. *Cymbidium echinocarpon* (Sw.) Sw., Nov. Acta Reg. Soc. Sci. Upsal. 6:71. 1799. *Dichaea echinocarpa* (Sw.) Lindl., Gen. & Sp. Orch. Pl. 208. 1833, nom. illeg. Type: JAMAICA: *Swartz s.n.* (holotype: BM). = **Dichaea pendula** (Aubl.) Cogn.

Pachyphyllum haemathodes (Ruiz & Pav.) Schltr., Repert. Spec. Nov. Regni Veg.Beih. 9:180. 1921. *Fernandezia haemathodes* Ruiz & Pav., Syst. Veg. Fl. Peruv. & Chil. 1:240. 1798. Type: PERU. Dept. Huanuco: Muña, *Pavon s.n.* (holotype: MA) = **Maxillaria haemathodes** (Ruiz & Pav.) Garay.

Pachyphyllum pamplonense Kraenzl., Pflanzenr. 4, 50:27. 1923. Type: COLOMBIA: Pamplona to Las Vetas, 3300 m, *Funk & Schlim s.n.* (holotype: W) = **Maxillaria nubigena** (Rchb.f.) C. Schweinf.

Pachyphyllum procumbens Lodd. ex W. Baxt., Loud. Hort. Brit. Suppl. 3:607. 1850, nom. nud.

Pachyphyllum ?scandens Llave & Lex., Nov. Gen. 2:17. 1824. TYPE: MEXICO: Huandacareo, Sep (HOLOTYPE: preserved?) = **Barkeria scandens** (Llave & Lex.) Dressler & Halbinger

Comment.—No Lexarza specimens are known to be extant.

Pachyphyllum subbiflorum (Ruiz & Pav.) Schltr., Repert. Spec. Nov. Regni Veg. Beih. 9:181. 1921. TYPE: PERU. DEPT. HUANUCO: Muña, *Pavon s.n.* (HOLOTYPE: MA) = **Fernandezia subbiflora** Ruiz & Pav.

Pachyphyllum steyermarkii Foldats, Acta Bot. Venez. 3:369. 1968. TYPE: VENEZUELA. Edo. Tachira: Tamá, 2475–2550 m, *Steyermark & Dunsterville* 98345 (HOLOTYPE: VEN) = **Fernandezia sanguinea** (Lindl.) Garay & Dunsterv.

Pachyphyllum uniflorum Llave & Lex., Nov. Veg. Descr. 2:25. 1824. TYPE: MEXICO: Irapeo (HOLOTYPE: preserved?). = **Barkeria uniflora** (Llave & Lex.) Dressler & Halbinger.

Comment.—No Lexarza specimens are known to be extant.

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REPASKY, R. and E.A. CHRISTENSON (In Press). Orchids of Peru: *Pachyphyllum pectinatum*. Orchid Review.

SENGHAS, K. 1995. *Orchidotypus*. Schlechter's Die Orchideen, ed. 3, I/B(31):1922–1924.

SZLACHETKO, D.L., J.M. EJSMONT, and P. RUTKOWSKI 2007. *Pachyphyllum piesiki* Szlach. spec. nov. (Vandoideae, Pachyphyllinae), eine neue Art aus Ecuador. Orchidee (Hamburg) 58:93–97.

BOOK REVIEWS

Brian L. Fisher and Stefan P. Cover. 2007. **Ants of North America: A Guide to the Genera.** (ISBN 978-0-520-254220, pbk.). University of California Press, 2120 Berkeley Way, Berkeley, California 94704, U.S.A. (**Orders:** California Princeton Fulfillment Services, 1445 Lower Ferry Road, Ewing, New Jersey 08618, U.S.A., www.ucpress.edu, 1-609-883-1759, 1-609-883-7413 fax). $34.95, 194 pp., line drawings, color photographs, 4 1/3" × 7".

Contents.—Preface, **1)** Introduction, **2)** Key to North American Ant Genera Based on the Worker Caste, **3)** Taxonomic Descriptions, **4)** Subfamily Descriptions, **5)** Genus Descriptions, **6)** Ant Genera of North America by Subfamily, **7)** Ant Species North of Mexico: A Working List, **8)** Terminology. Identification References, General References, Index.

As prevalent as ants are in the environment, it has been difficult to find guides to lead to their identification. This handy field guide fulfills that need with an excellent key that provides line drawings of features described, followed by color photographs of a species representative of each genus, and descriptions of the genera. Neither the key nor the diagnostic remarks are for the fledgling amateur or the easily daunted, as some knowledge of ant morphology is almost essential. Still, ant-identifiers must be determined and with the helpful terminology section can master the key. Of interest even to the general reader is the "distribution and ecology" of each genus, which offers fascinating facts about these insects. A working list of species north of Mexico and references to all the genera for further reading complete this important field guide.—*Joann Karges, Texas Christian University Library (retired), Fort Worth, Texas, U.S.A.*

Jay H. Buckley. 2008. **William Clark: Indian Diplomat.** (ISBN 978-0-8061-3911-1, pbk.) University of Oklahoma Press, **2800 Venture Drive, Norman, Oklahoma 73069-8218, U.S.A.** (**Orders:** www.oupress.com, **1-800-627-7377**, 1-**800-735-0476 fax**). $29.95, 320 pp., b/w illustrations, maps, 6" × 9".

Following his return to St. Louis from the infamous expedition to explore a trade route to the Pacific, William Clark spent three decades as an agent of the US Government's Indian Policy. First as an Indian Agent, then as Territorial Governor of Missouri and finally Superintendent of Indian Affairs, he was responsible for 10% of all treaties signed by Indian and Government leaders. Ironically, Clark's paternalism toward the Indian ultimately resulted in relocation of more Native Americans than any other government agent.

Lewis and Clark enthusiasts and others interested in the expansion of the American West will relish this thoroughly researched biography of William Clark. Jay H. Buckley draws upon Clark's extensive papers as well as published government archives to explore this extremely skilled and complex American diplomat. Respected equally by Indian and US government leaders, many Indian chiefs would not consider a treaty legitimate unless personally endorsed by Clark.—*Gary Lee Hinds, Rio Brazos Master Naturalist and BRIT volunteer, Fort Worth, Texas, U.S.A.*

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LECTOTYPIFICATION AND NOTES ON *BACCHARIS RIOGRANDENSIS* (ASTERACEAE: ASTEREAE)

Gustavo Heiden
B. Sc., CNPq-PROTAX Fellow
Escola Nacional de Botânica Tropical/Instituto de Pesquisas Jardim Botânico do Rio de Janeiro
Pacheco Leão, 915, Jardim Botânico
Rio de Janeiro, RJ 22460-030, BRAZIL
gustavo.heiden@gmail.com

Angelo A. Schneider
M. Sc., Programa de Pós-Graduação em Botânica
Universidade Federal do Rio Grande do Sul
Av. Bento Gonçalves
9500, Porto Alegre, RS 91501-970, BRAZIL
angeloschneider@yahoo.com.br

ABSTRACT

Baccharis riograndensis Malag. & J.E. Vidal, an endemic species from southern Brazil, was described based on two syntypes and two paratypes. Until now, no lectotype was designated. Study of original material and a major number of other herbarium materials confirm the distinctiveness of the taxon. *Baccharis riograndensis* is lectotypified and additional data, including a diagnostic description, illustrations, specimen citations, geographic range map and IUCN (2001) status of conservation are presented.

RESUMO

Baccharis riograndensis Malag. & J.E. Vidal, uma espécie endêmica do sul do Brasil, foi descrita com base em dois síntipos e dois parátipos. Embora a espécie tenha sido citada em vários trabalhos, nenhuma lectotipificação foi feita até o momento. O estudo do material original em conjunto com a revisão de coleções em herbários confirmou a individualidade do táxon. *Baccharis riograndensis* é lectotipificada e dados adicionais, incluindo uma descrição diagnóstica, ilustrações, distribuição geográfica e estado de conservação, segundo os critérios da IUCN, são apresentados.

Baccharis riograndensis Malag. & J.E. Vidal, an endemic species from Rio Grande do Sul State, in southern Brazil, was described by Malagarriga (1949, under his monk name Irmão Teodoro Luis) based on two specimens collected by J.E. Vidal (syntypes) and two collections (paratypes) made by Malagarriga himself. After the publication, accounts of this species appeared in the taxonomic literature several times (Malagarriga 1957, 1958, 1977; Barroso 1976; Diesel 1987; and Oliveira et al. 2007), but no lectotypification was made.

The study of the syntypes housed at Herbarium R, Museu Nacional do Rio de Janeiro, along with general collections from various herbaria, confirmed this taxon as distinct and allowed a choice of lectotype. Along with the lectotypification, additional data are presented, including a morphological description, illustration, specimen citations, geographic distributional map, and IUCN (2001) status of conservation.

Baccharis riograndensis Malag. & J.E. Vidal, Bol. Inform. Inst. Geobiol. 1:13. 1949. **(Fig. 1)**. Type: BRASIL. Rio Grande do Sul: Santa Maria, Boca do Monte, Mar 1939, ♀, *J.E. Vidal 37006* (lectotype, designated here: R!).

Diagnostic description.—Subshrub, 25–65 cm tall. Stems mostly erect, sometimes short reptant and decumbent, 3-alate, indument of clavate uniseriate hairs in tufts, wings of vegetative branches undulate, 0.5–5 cm long, 0.25–0.75 cm wide, fertile branches distinctly winged, wings narrower, 0.1–0.2 cm wide. Leaves reduced to scales 0.1–0.2 cm long, 0.1–0.25 cm wide. Capitulescence a panicle of pseudospikes, 5–25 cm long, lateral spikes reduced to solitary sessile capitula, not arranged in glomerules. Male capitulum: involucre campanulate 3.5–5.5 mm long, 3.5–4 mm wide, phyllaries in 4–5 series, the outer oblong, the mediums ovate, the inner short lanceolate, apex obtuse, margins narrowly hyaline, entire to short toothed apically. Flowers 18–30 [40], pappus 4–5 mm long, uniseriate, 20–22 bristles, corolla 3–5 mm long, apically 5-lobed, tube 2.8–3.3 mm, throat 0.2–0.3 mm, lobes 1.5–2 mm, style 4–5 mm long, style apex not divided. Female capitulum: clinanthium alveolate, bearing biseriate hairs, involucre cylindrical, 7–10 mm long, 2–3 mm wide, phyllaries in 4–7 series, the outers short ovate becoming more linear onwards the innermost series, apex acute, margins narrowly hyaline, entire to short toothed apically. Flowers 30–40, pappus 7–8 mm

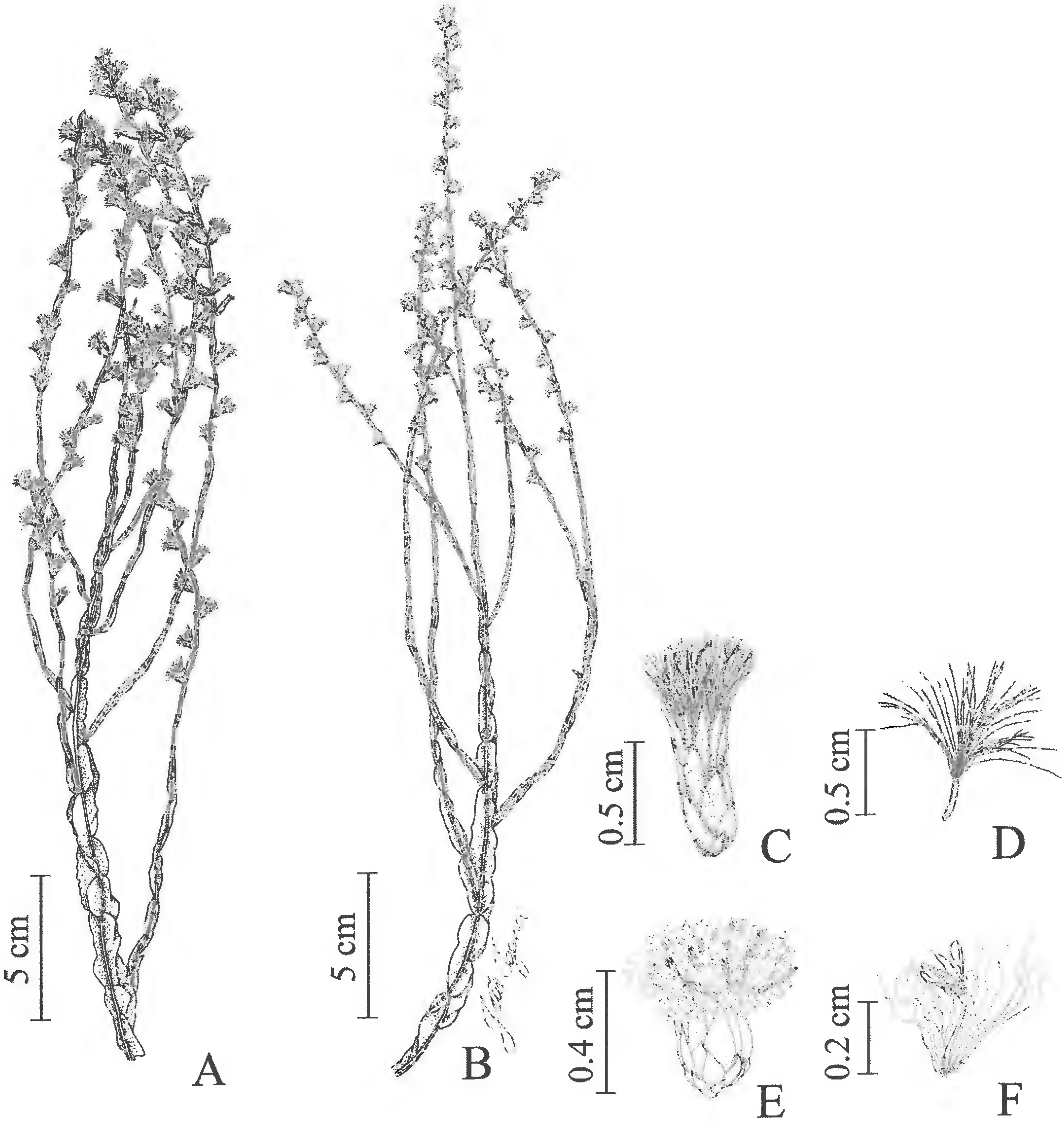

Fig. 1. *Baccharis riograndensis*. A. Habit of female plant, B. Habit of male plant, C. Female capitulum, D. Female flower, E. Male capitulum, F. Male flower. *G. Heiden 648* (A, C and D); *G. Heiden 649* (B, E and F).

long, uniseriate, corolla 5–7 mm long, ligulate with the ligule 5- toothed, style 7–7.5 mm long, cypselas 2.5–4 mm long, cylindrical, 12–20 ribbed, surface few papillose and glabrous. Chromosome number $2n$ = 18 (Heiden et al. 2006).

Etymology.—The name of the species refers to the type locality.

Vernacular names.—carqueja, chirca.

Phenology.—Fertile between December and March; dispersion of cypselas may last until June.

Geographic range.—Known only from the state of Rio Grande do Sul, Brazil (Fig. 2).

Conservation.—Although an endemic with restricted area in Rio Grande do Sul, the species is abundantly found in dry or rocky grasslands, mainly in the southern half of the state (granite sites in the Pampa biome),

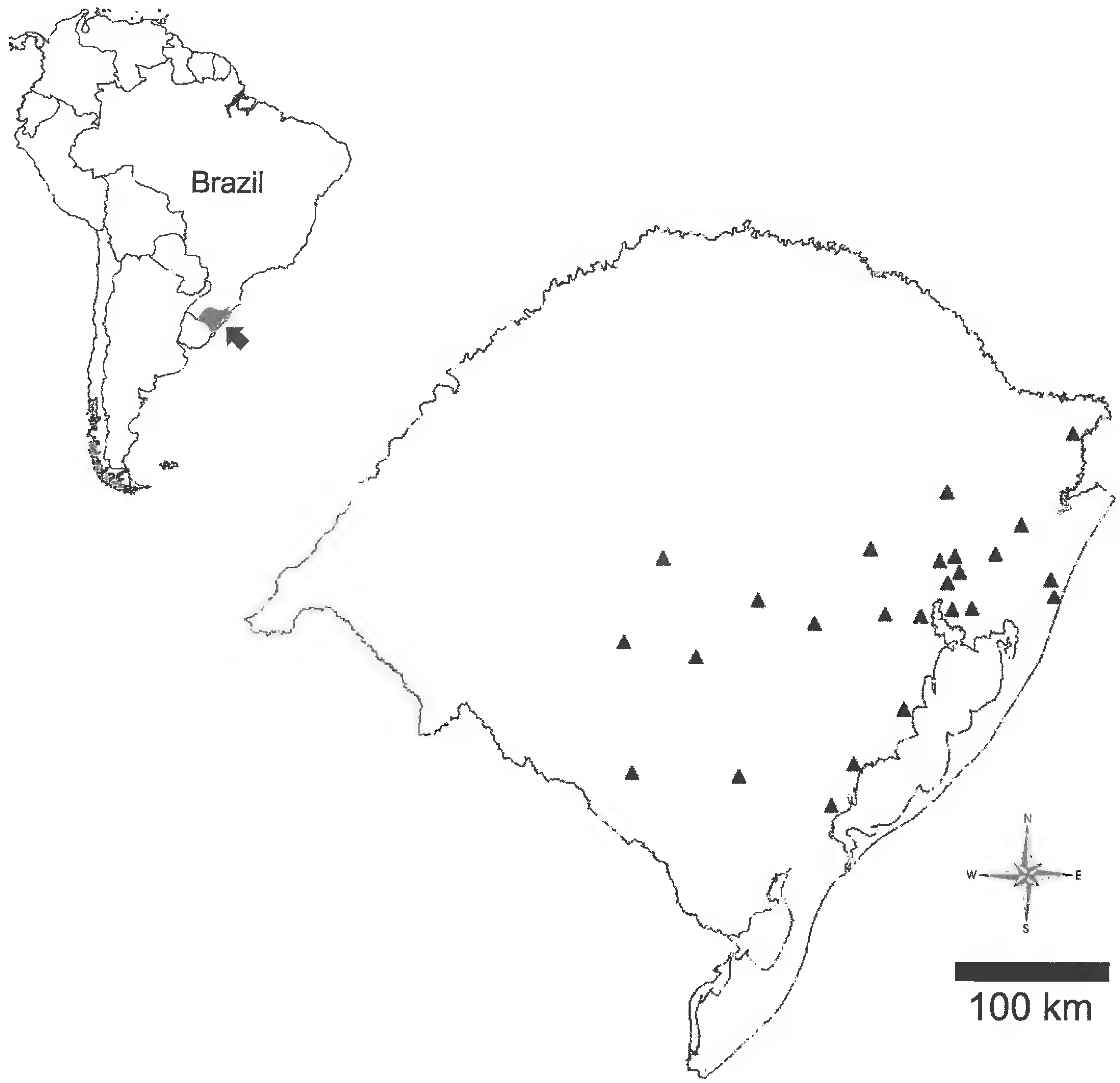

Fig. 2. Geographic range of *Baccharis riograndensis* (Asteraceae, Astereae) in Rio Grande do Sul State, southern Brazil.

and sparsely in the northern half (islands of discontinuous grassland areas on plateau sites inserted in the Atlantic Forest biome). Increasing land use and planned forest projects may disrupt the habitat of the species. Due to the anthropogenous pressure on the south Brazilian subtropical grasslands (*campos*) with the increasing of displacement of native vegetation in substitution to large-scale *Eucalyptus* and *Pinus* plantations, the species is regarded as Near Threatened (NT), concerning the IUCN (2001) status of conservation.

Comments.—*Baccharis riograndensis* is assigned to subgen. *Molina* Heering and sect. *Caulopterae* DC., to the latter mainly due to presence of winged stems, clinanthium with glandular hairs, and pappus bristles of female flowers that are enlarged basally and fused into a ring. *Baccharis riograndensis* is sympatric in its entire limited range to *Baccharis crispa* Spreng., which has a wider distributional area in southeastern South America. Similar characteristics to the both species are the similar habitat, erect branches with undulate wings, involucre of male capitula campanulate and uniseriate pappus in male and female flowers. *Baccharis riograndensis* differs from *B. crispa* due to the fertile branches distinctly narrow-winged (vs. not distinctly winged fertile branches), lateral spikes reduced to solitary capitula (vs. lateral spikes fully developed or

with reduced axis seeming glomerules), involucre of female capitula cylindrical (vs. campanulate) and larger cypselas, 2.5–4 mm long (vs. smaller, 1–1.5 mm long). Another taxon, similar to *B. riograndensis*, is the alopatric *Baccharis genistelloides* subsp. *lorentzii* Joch. Müll., from central Argentina, which shares some characteristics with *B. riograndensis*, such as the pseudospikes with the lateral spikes generally reduced to one capitulum, cylindrical involucre of female capitula and larger capitula and cypselas, but differs on the basis of its erectopatent branching (vs. erect), usually narrower capitulescences (vs. wider), fertile branches not distinctly winged (vs. distinctly narrow-winged fertile branches), fewer cypsela ribs (9–12 vs. generally 12–20) and multiseriate pappus (vs. uniseriate).

Representative specimens: **BRAZIL. Rio Grande do Sul: Arroio dos Ratos:** Fazenda Faxinal, 10 Mar 1977, *K. Hagelund 10967* (ICN); Fazenda Faxinal, 13 Feb 1978, *K. Hagelund 12057* (ICN). **Bagé:** BR-153, km 84, 1 June 1985, *M. Sobral & C. Grabauska 3920* (ICN); Casa de Pedra, 12 Apr 1991, *M.R. Ritter 612* (ICN); começo do Passo do Enforcado, 70 km NE de Bagé, 5 Mar 1981, *J.C. Lindeman et al. 6997* (CNPO); Passo do Velhaco, 21 Mar 2001, *V. Marin 20* (CNPO); ponte sobre o Arroio Traíras, RS-153, 28 Mar 1985, *O. Bueno 4312* (HAS). **Caçapava do Sul:** à 8 km da rodovia para Bagé, 10 Mar 1982, *J. Mattos 23628* (HAS); à 8 km da rodovia para Bagé, 10 Mar 1982, *J. Mattos & N. Mattos 23630* (HAS). **Caxias do Sul:** Ana Rech, 12 Feb 2000, *A. Kegler 678* (HUCS). **Cachoeira do Sul:** Cerro dos Peixoto, 1 Apr 1985, *M. Sobral 3783a* (ICN). **Canoas:** 16 Feb 1949, *Irmão Teodoro Luis s.n.* (ICN 17068, 17069). **Guaíba:** BR-116, km 32, 13 Mar 1993, *N.I. Matzenbacher s.n.* (ICN 53681). **Osório:** Faz. do Arroio, 14 Apr 1950, *B. Rambo s.n.* (PACA 46796). **Pântano Grande:** ant. Fazenda Capivarita, 26 Feb 1990, *G. Grazziotin et al. s.n.* (HUCS 6591). **Pelotas:** Cerrito Alegre, 8 Mar 1956, *O. Pereira s.n.* (ICN 1469). **Piratini:** Fazenda São João, 8 Apr 1991, *R. Wasum et al. s.n.* (HUCS 7575, 7576). **Portão:** 17 Mar 1986, *S. Diesel s.n.* (HUCS 3750). **Porto Alegre:** Jardim Botânico, 11 Mar 1980, *O. Bueno 2193* (HAS); Jardim Ingá, 4 Apr 1992, *L.T. Pereira 1* (ICN); Morro das Abertas, 26 Mar. 1980, *O. Bueno 2281* (HAS); [idem]. 08 Apr 1980, *O.Bueno 2337* (RB); [idem], 26 Mar 1980, *O.Bueno 2281* (RB); Morro do Osso, 25 May 1992, *L.T. Pereira 14* (ICN); Morro Santana, 16 Mar 1967, *A.G. Ferreira 139* (ICN). **Santa Maria:** Boca do Monte, Mar 1939, ♂, *J.E. Vidal 37004* (R); 24 May 1960, *Irmão Teodoro Luis s.n.* (SMDB 876, 884). **São Francisco de Paula:** entrada para a Serra do Umbu, 1 km, 12 Mar 1994, *L.T. Pereira 96* (ICN); Fazenda Mulita, 9 Apr 2001, *R. Wasum 1049* (HUCS). **São Gabriel:** 73Km da saída de São Gabriel, 27 Mar 1985, *O. Bueno 4277* (HAS). **São José dos Ausentes:** Silveira, Fazenda do Tabuleiro, 18 Mar 2002, *R. Wasum 1405* (HUCS). **São Leopoldo:** ad montem Sapucaia, 09 Mar 1949, *B. Rambo s.n.* (PACA); Quinta, 10 Mar 1937, *J. Dutra 1536* (ICN). **São Lourenço do Sul:** Passo dos Baios, 25 Feb 2004, *G. Heiden 421* (HECT, PEL); [idem], Mar 2006, *G. Heiden 648* (RB); *G. Heiden 649* (RB). **São Sebastião do Caí:** Vila Rica, 9 Mar 1985, *S. Diesel s.n.* (PACA 68069). **Sapucaia do Sul:** Morro Sapucaia, 23 Apr 1979, *O. Bueno 1295* (HAS). **Taquara:** 07 Apr 1957, *J. Mattos 6803* (PACA). **Tramandaí:** Parque Osório, 04 Mar 1994, *L.T. Pereira 82* (ICN). **Viamao:** *J. Mattos 2249* (HAS).

Selected additional specimens:
Baccharis crispa Spreng. **URUGUAY. Montevideo:** 1821–1822, ♂, *Sellow d397* (isotype: R).
Baccharis genistelloides subsp. **lorentzii** Joch. Müll. **ARGENTINA. Buenos Aires:** "Sierras Pampeanas," Arroyo Pigue, 22 Mar 1881, ♂, *Lorentz s.n.* (SP 25365; 25368).

ACKNOWLEDGMENTS

Authors acknowledge the herbaria CNPO, HAS, HASU, HECT, HUCS, HURG, ICN, PACA, PEL, R, RB, SMDB, and SP; Guy L. Nesom and Jochen Müller for the helpful comments; and João Ricardo Vieira Iganci for providing the illustration.

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BOOK REVIEW

ANTONY WILD. 2005 (American Edition). **Coffee: A Dark History.** (ISBN 0-393-06071-3, hbk.). W.W. Norton & Company, Inc., 500 5th Avenue, New York, New York 10110, U.S.A. (**Orders:** www.wwnorton.com, 1-800-233-4830, 1-800-458-6515 fax). $25.95, 323 pp., 8 plates (7 color, 1 b/w), 6 3/8" × 9 1/2".

Contents.—Preface, Prologue, **1)** The Way We Live Now, **2)** Origins, **3)** Enter the Dragon, **4)** The Mocha Trade, **5)** Coffee and Societies, **6)** The Fall of Mocha, **7)** Slavery and the Coffee Colonies, **8)** The Continental System and Napoleon's Alternative to Coffee, **9)** Napoleon and St Helena, **10)** Slavery, Brazil, and Coffee, **11)** The Great Exhibition, **12)** Harrar and Rimbaud: the Cradle and the Crucible, **13)** Modern Times, **14)** Coffee, Science, and History, **15)** The Battle of the Hemispheres, **16)** Fair Trade, **17)** Espresso: the Esperanto of Coffee, **18)** The Heart of Darkness. Coda, Appendix: The Find at Kush, Selected Further Reading, Index.

Coffee: A Dark History begins with an ominous tone in the prologue and downshifts to an outright disastrous tone by the first chapter. Here, author Antony Wild bemoans the plight of small Third World coffee growers as pawns in the greedy clutches of the world's advanced, mega-consumer countries. Anticipating a politically charged assault in the second chapter, I was delighted when Wild turned his engaging writing style to the very roots of coffee history. He begins with the evolutionary development of humans as a species and brings in some very interesting coffee-related possibilities. His jumping off point for such musing is the supposed origins of humans and coffee in the area now know as Ethiopia. Taking history a little farther along, he even puts forth coffee as the forbidden fruit of the Garden of Eden. He goes on to hypothesize coffee's earliest possible use and cultivation by various cultures as early as the 15th century. He also sprinkles in botanical/scientific facts about coffee along the way.

The first two-thirds of the book continues and expands on the role of coffee in political struggles, colonialism, imperialism, economics and culture, and social development. Botanical and other scientific tidbits are always present. This book is a great way to read through world history as a very organic, intertwined story. The last third of the book resumes with the late 18th century and takes you through to present day. Though the dark history of coffee is a theme throughout, its evilness, according to Wild, has achieved epic proportions in the present day. And though the author, once a coffee trader himself, eschews the coffee giants and predicts world catastrophe around coffee trade atrocities, he does include a slightly positive chapter on fair trade coffee. Despite coffee's dark history, Wild has written a fascinating, well-researched, and utterly intriguing treatise.—*Robert J George, Botanical Research Institute of Texas, 500 East 4th Street, Fort Worth, Texas 76102-4025, U.S.A.*

NEW SPECIES OF MYRTACEAE FROM ECUADOR

Bruce K. Holst
Marie Selby Botanical Gardens
811 South Palm Avenue
Sarasota, Florida 34236, U.S.A.
bholst@selby.org

Maria Lúcia Kawasaki
Department of Botany
Field Museum of Natural History
1400 South Lake Shore Drive
Chicago, Illinois 60605-2496, U.S.A.
lkawasaki@fieldmuseum.org

ABSTRACT

Four new species of Myrtaceae from Ecuador are described and illustrated: **Calyptranthes websteri, Eugenia concava, Eugenia grossa,** and **Myrcia subcordifolia.**

RESUMEN

Se describen y se ilustran cuatro especies nuevas de Myrtaceae del Ecuador: **Calyptranthes websteri, Eugenia concava, Eugenia grossa,** y **Myrcia subcordifolia.**

INTRODUCTION

In preparation for the treatment of Myrtaceae for the Flora of Ecuador, four new species have been recognized and are here described and illustrated: *Calyptranthes websteri, Eugenia concava, Eugenia grossa,* and *Myrcia subcordifolia.*

Calyptranthes websteri B. Holst & M.L. Kawasaki, sp. nov. (**Fig. 1**). Type: ECUADOR. Pichincha: Canton Quito, Parroquia Nanegal, Bosque Protectora Maquipucuna, Montañas de Maquipucuna, rain forest on main ridge of Cerro Sosa, ca. 7 km airline SE of Nanegal, 2150 m, 00°04.5'N, 78°36.5'W, 8 Jul 1992 (fl), *G.L. Webster, F. Hrusa & C. Zurinsky 29164* (holotype: DAV; isotypes: AAU, SEL).

Arbor, indumento minute dibrachiato rubello; foliis 13.6–20.2 × 6.1–9.4 cm, ellipticis vel leviter ovatis vel obovatis, caudatis, venis mediis supra concavis, venis marginalibus 2–6 mm remotis; petiolis 9–13 mm longis; paniculis multifloris, pedunculis et pedicelis longis et gracilibus; alabastris ca. 5 mm longis, petalis absentibus.

Tree to 10 m tall or scrambling tree; trichomes dibrachiate, minute, with very short arms, reddish, abundant on new growth; branchlets terete to slightly compressed. **Leaf blades** generally elliptic to very slightly ovate or obovate, 13.6–20.2 × 6.1–9.4 cm, chartaceous when dry, bearing scattered trichomes, these deciduous with age, olive green to brown on upper surface when mature, lighter yellow green on lower surface, immature leaves with slightly yellowish grey pallor due to waxy layer; apex caudate, the tip 7–19 mm long, margins slightly revolute; base attenuate to cuneate; midvein impressed on upper surface, convex and slightly prominent on lower surface; lateral veins 19–26 pairs, flat on upper and convex on lower surfaces, principal marginal vein 2–6 mm distant from the edge, slightly less prominent than the lateral veins, secondary marginal vein ca. 1 mm from edge, faintly evident; glands scattered, translucid on both surfaces; petiole 9–13 mm long, ca. 2 mm thick, margins inrolled and meeting to form a tunneled petiole. **Inflorescences** paniculate, decompound, many-flowered, 2 or 4 borne together on abortive branches, when young, densely covered by a light gray-tan waxy bloom over the small, appressed trichomes; bracts early deciduous, ca. 8 × 1 mm; peduncles 1–5 cm long, the first node bearing 3 or 5(7) branches and upper nodes bearing usually 3 branches, all branches from single node in same plane, the branches terminating with 3 long-pedicellate flowers, the terminal one sometimes abortive; pedicels 18–37 mm long; bracteoles early deciduous, 3–4 mm long. **Flowers:** buds globose, ca. 5 × 5 mm, with a light gray-tan waxy bloom, particularly on lower 2/3 of bud; calyptra ca. 3 × 5 mm, generally lighter in color than hypanthium, apiculum barely evident; petals lacking; stamens numerous; filaments ca. 6 mm long; anthers ca. 0.5 mm long; style ca. 5 mm long; hypanthium ca. 4 mm long, the free portion ca. 2 mm long; ovary 2-locular, ovules 2 per locule. **Fruits** not known.

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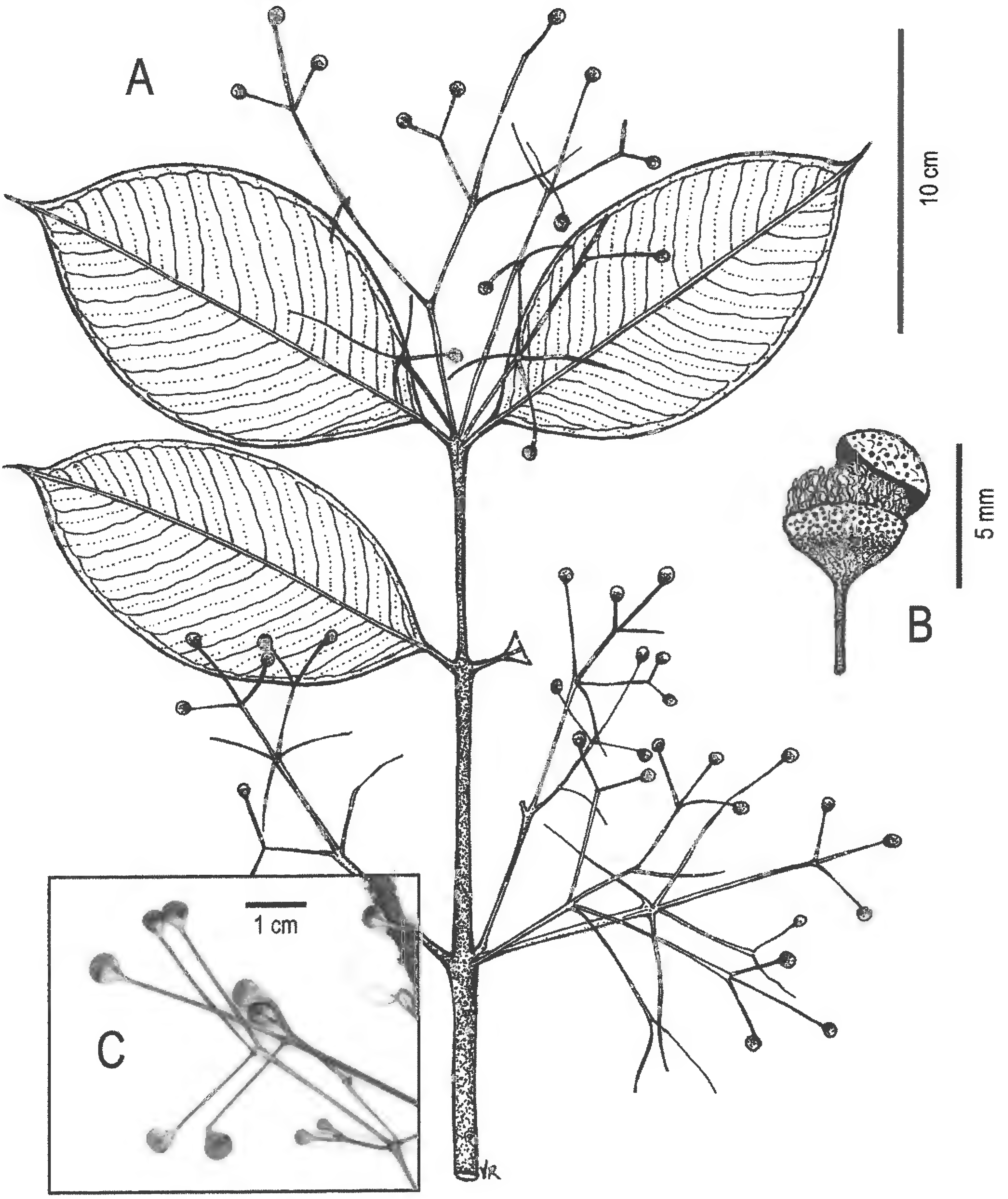

Fig. 1. *Calyptranthes websteri* B. Holst & M.L. Kawasaki: A. Habit. B. Flower. C. Digital scan of flower buds. (A–C, *Webster et al. 29164*).

Distribution.—Known only from Maquipucuna, Pichincha province, in primary rain forests at 2100–2150 m elevation.

Calyptranthes websteri is distinguished from all other Andean species by the elongate peduncles and pedicels of the many-flowered inflorescence. This very distinctive species is named in memory of its discoverer, Grady Webster, an astute student of the Euphorbiaceae and respected teacher at the University of California, Davis, who passed away in 2005.

Additional collection examined: **ECUADOR. Pichincha:** Canton Quito, Parroquia Nanegal, Bosque Protectora Maquipucuna, Montañas de Maquipucuna, Cerro Sosa, primary rain forest on main ridge, 2100–2150 m, 00°05'N, 78°37'W, 9 Jul 1991 (fl), *G.L. Webster et al. 28884* (AAU, DAV, MO, QCNE).

Eugenia concava B. Holst & M.L. Kawasaki, sp. nov. (**Fig. 2**). TYPE: ECUADOR. GUAYAS: Guayaquil, Bosque Protector Cerro Blanco, road Guayaquil–Salinas, Km 15, 200–300 m, 02°10'S, 80°08'W, Jan 1994 (fl), *T. Núñez & A. Hernández 197* (HOLOTYPE: QCNE; ISOTYPES: MO, SEL).

Frutex vel arbor; foliis plerunque ellipticis, chartaceis, glabris, abrupte acuminatis, nervo medio supra prominente; floribus fasciculatis, pedicellis gracilibus; calycis lobis concavis; fructis ellipsoideis.

Shrub or tree, 2.5–10 m tall, mostly glabrous; twigs smooth, trunk and older branches with bark peeling in plates or strips. Leaf **blades** mostly elliptic, less commonly ovate or obovate, chartaceous, 4–7.5 × 2.5–4 cm, drying olive green or greenish brown; upper and lower surfaces glabrous; glands punctiform, plane or slightly salient on both surfaces; midvein convex on the upper surface; lateral veins 10–12 pairs, salient on both surfaces; marginal veins 2, the innermost slightly arched, 1–3 mm from the margin; base usually obtuse, rarely cuneate; apex abruptly acuminate, the acumen ca. 1 cm long; petioles 2–3 mm long, flattened, glabrous. **Inflorescences** appearing fasciculate, with up to 4 flowers, axillary or subterminal, the pedicels 1–1.5 cm long, slender, glabrous; bracteoles ovate, ca. 1 mm long, ciliate, persistent. **Flowers** 4-merous, buds ca. 5 mm long; hypanthium ca. 2 mm long, glabrous; calyx-lobes ovate to lanceolate, 3–4 mm long, obtuse, concave, glabrous; petals suborbicular, ca. 4 mm diam., ciliate or glabrous; disk ca. 3 mm diam., glabrous; stamens ca. 5 mm long; style ca. 6 mm long; ovary 2-locular, ovules several per locule. **Fruits** berries, ellipsoid, 1–1.5 × 0.8–1 cm, glabrous, red, gland-dotted; seed 1, ca. 9 × 6 mm, the seed coat membranous; embryo eugenioid, the cotyledons fleshy, connate, the radicle indistinct.

Distribution.—*Eugenia concava* is known only from Guayas province, occurring in dry forests at 200–500 m elevation.

Eugenia concava is characterized by small, elliptic, glabrous leaves, abruptly acuminate at apex, the midvein convex on the upper surface; the inflorescences are fasciculate, with slender pedicels and flowers with concave calyx lobes. The pulp is characterized as "sweet" by Palacios & Rubio (*9977*). *Eugenia concava* resembles *E. rhombea* Krug & Urb., a species from Southern Florida, Mexico, Central America, and West Indies (McVaugh, 1989), but differs by the leaves with distinctly convex midvein (vs. concave), lacking a distinct cartilaginous leaf margin (vs. present), and by the ellipsoid fruits (vs. globose).

Additional collections examined: **ECUADOR. Guayas:** Bosque Protector Cerro Blanco, 350 m, 02°10'S, 79°58'W, 16 Jan 1994 (fl), *X. Cornejo & C. Bonifaz 1387* (SEL); Guayaquil, Bosque Protector Cerro Blanco, 15 km W of Guayaquil, near Quebrada Papagayo, 230 m, 02°10'S, 79°58'W, 27 May 1996 (fr), *D. Neill & T. Núñez 10474* (F, MO, SEL); Guayaquil, Cerro Blanco, coastal road, Km 15, 350 m, 02°1'S, 79°58'W, 16 Mar 1992 (fr), *W. Palacios & D. Rubio 9944* (MO, SEL); Guayaquil, Cerro Azul, coastal road, Km 12, 500 m, 02°10'S, 79°58'W, 18 Mar 1992 (fr), *W. Palacios & D. Rubio 9977* (F, MO, QCNE, SEL); Guayaquil, Bosque Protector Cerro Blanco, road to Salinas, Km 15, 400 m, 02°10'S, 79°58'W, 21–25 Jan 1992 (fl), *D. Rubio & G. Tipaz 2321* (MO, SEL); Guayaquil, Bosque Protector Cerro Blanco, road to Salinas, Km 15, 400 m, 02°10'S, 79°58'W, 21–25 Jan 1992 (fl), *D. Rubio & G. Tipaz 2348* (MO, SEL).

Eugenia grossa B. Holst & M.L. Kawasaki, sp. nov. (**Fig. 3**). TYPE. ECUADOR. CARCHI: Tulcan Canton, Parroquia Tobar Donoso, Reserva Etnica Awá, Sector Sabalera, 650–1000 m, 01°00'N, 78°24'W, 18–28 Jun 1992 (fl, fr), *G. Tipaz, J. Zuleta & N. Guanga 1370* (HOLOTYPE: QCNE; ISOTYPES: F, MO, SEL).

Arbor, indumento aureo-brunneo; foliis 27–45 × 19–25 cm, ellipticis vel ovatis vel obovatis, venis mediis supra concavis, venis marginalibus 12–21 mm remotis; racemis 15–21 mm longis, 6-floris, pedicellis 1–4 cm longis, floribus ca. 13 mm longis.

Tree 6–15 m tall, pubescent to puberulent on new growth. **Leaf blades** elliptic to broadly elliptic, chartaceous, 27–45 × 19–25 cm, brown on upper surface, pubescent along veins, the lower surface evenly pubescent, trichomes short and golden brown; glands indistinct above, dark and numerous below; midvein broadly and shallowly concave on upper surface, all veins convex and prominent on underside (midvein extremely prominent); lateral veins 11–16 pairs, first lateral (or secondary) vein extending to form inframarginal vein and straightening out; marginal veins 3, the inner, most conspicuous vein 12–21 mm from blade margin, the middle marginal vein 2–6 mm from margin, and a 3rd inframarginal vein, very faint, ca. 1 mm from margin; apex acuminate; base rounded to obtuse to very slightly cordate; petioles 13–20 mm long, 4–6

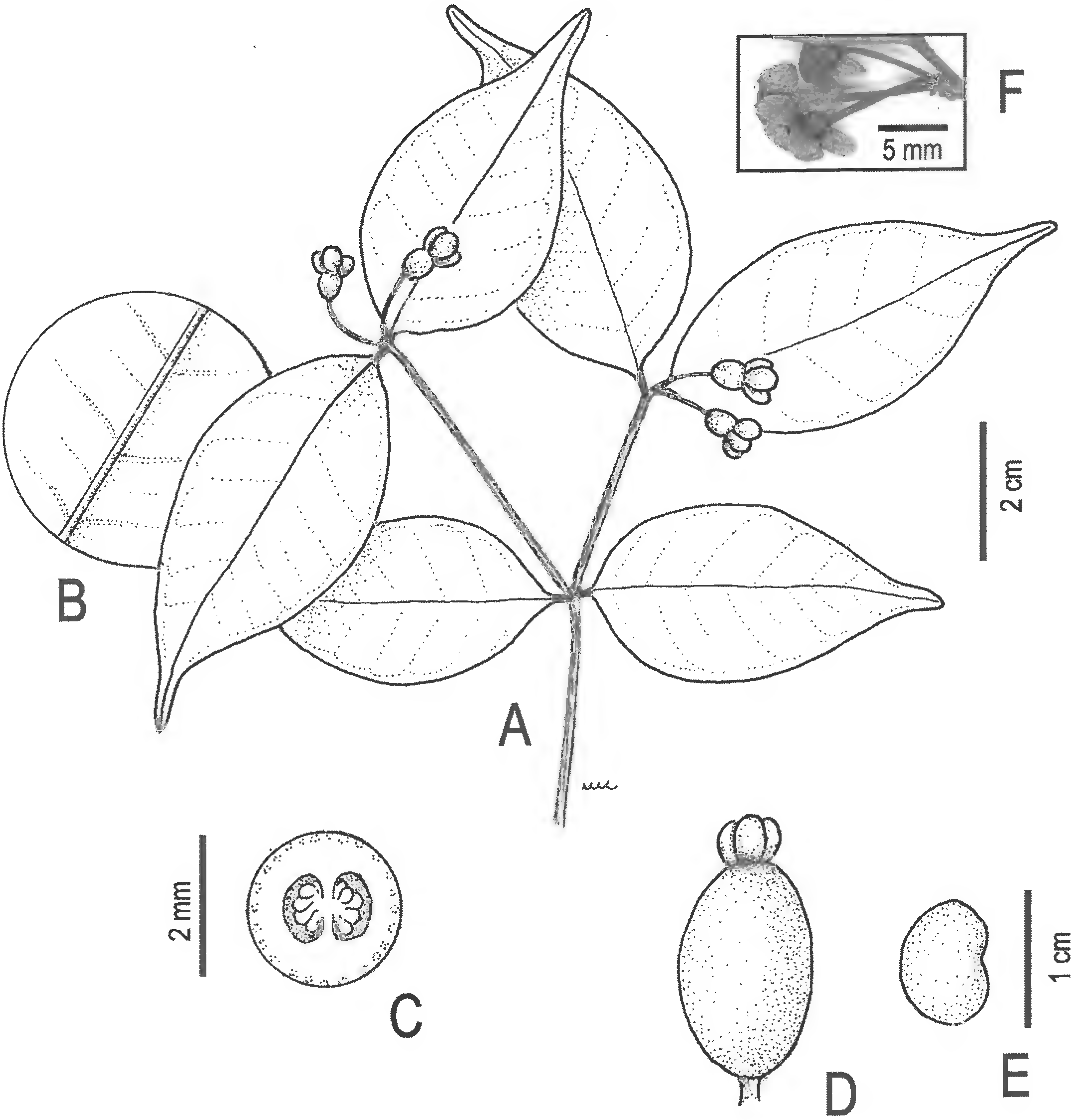

Fig. 2. *Eugenia concava* B. Holst & M.L. Kawasaki: A. Part of stem with leaves and young fruits. B. Detail of convex midvein on adaxial surface of leaves. C. Transversal section of ovary. D. Fruit. E. Embryo. F. Digital scan of flowers past anthesis (A–B, *Neill & Núñez 10474*; C, *Rubio & Tipaz 2348*; D–E, *Palacios & Rubio 9977*; F, *Nuñez & Hernández 197*).

mm diam., densely pubescent with golden trichomes. **Inflorescences** racemose, the axis 15–21 × 3–4 mm, pubescent, often at leafless nodes, 3 pairs of pedicels per peduncle; bracts deciduous; bracteoles fused and cupping hypanthium, 10–12 (14–15 hydrated) mm long, pubescent inside and out, deciduous after anthesis, pedicel in flower ca. 1 cm long, lengthening and thickening considerably in fruit, to 4 cm long. **Flowers** 4-merous, buds roundish, ca. 13 mm long; hypanthium abundantly pubescent inside and out, ca. 6 mm wide at summit, hypanthium after removal of bracteoles displaying slightly longer trichomes, having a hint of red or dark orange, apparent wrinkles or bumpy protrusions (some of which corresponding to marks on inner surface of bracteoles); outer calyx lobes suborbicular, ca. 9 × 9 mm, the inner lobes more closely ovate, ca. 10 × 7 mm, the tip acute (with triangular or acuminate shaped discoloration or mark, perhaps where

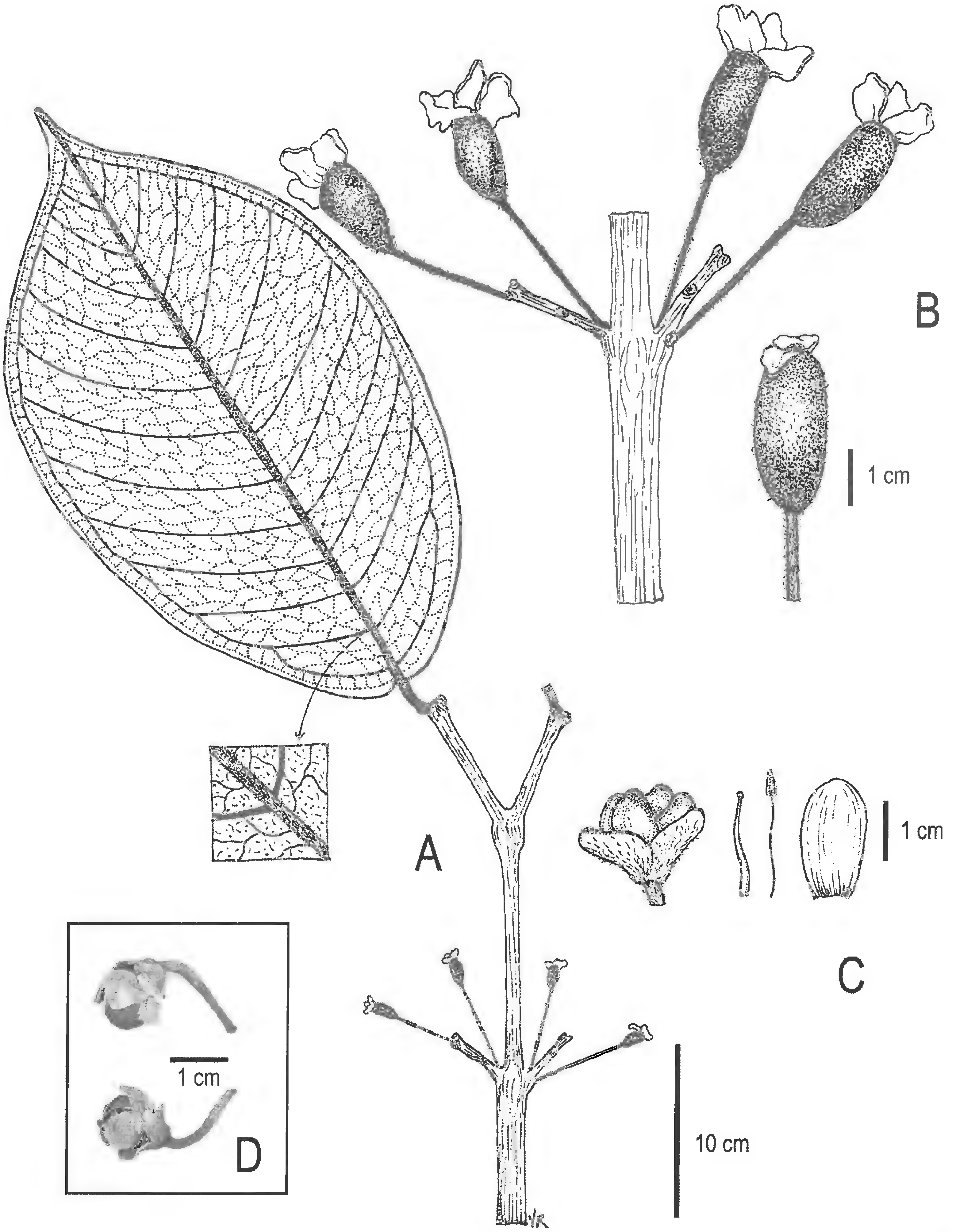

Fig. 3. *Eugenia grossa* B. Holst & M.L. Kawasaki: **A.** Branch habit. **B.** Young fruits. **C.** Flower bud, style and stigma, stamen, petal. **D.** Digital scan of flower buds. (A–B, *Aulestia et al. 830*; C–D, *Tipaz et al. 1370*).

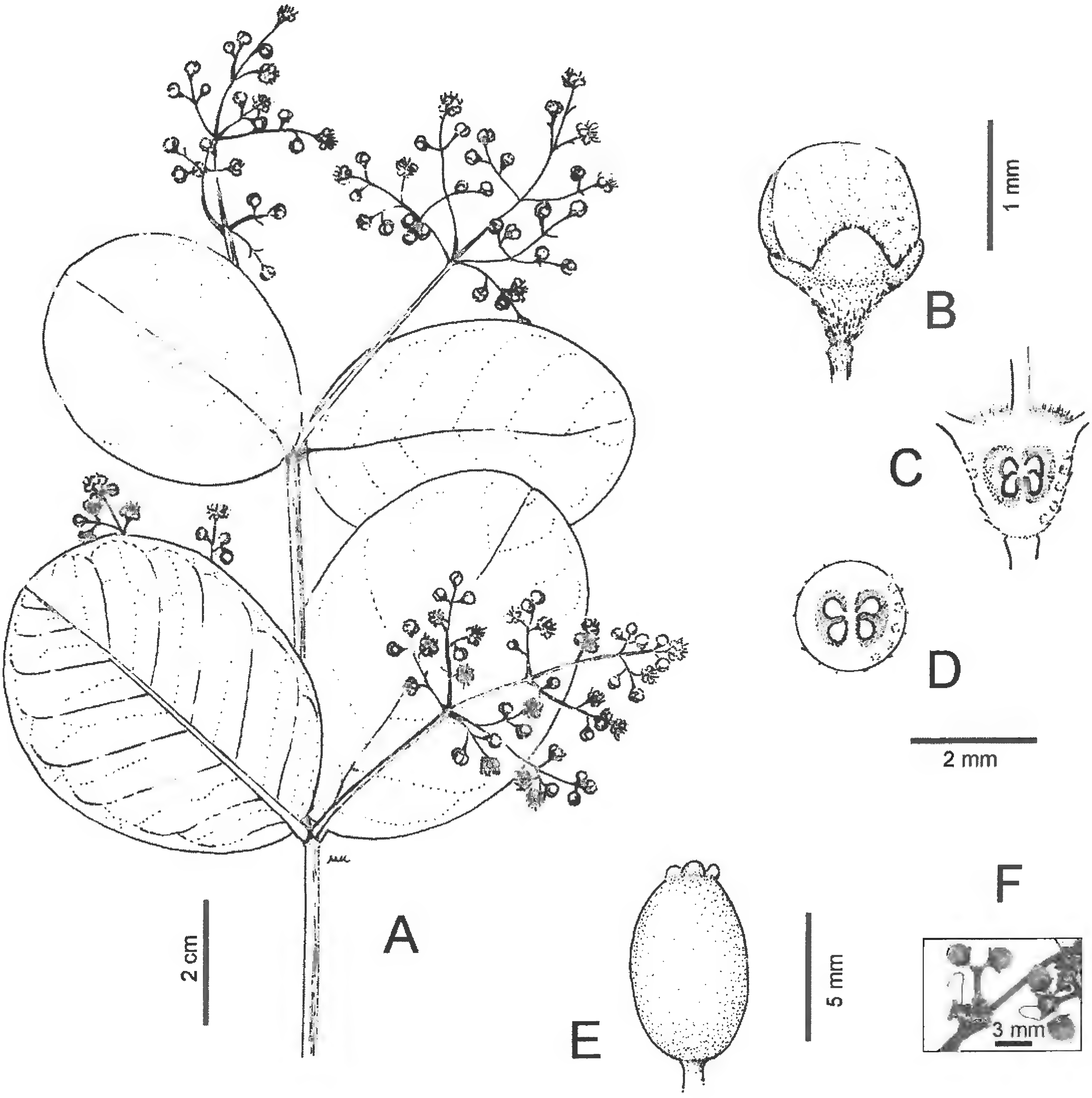

Fig. 4. ***Myrcia subcordifolia*** **B. Holst & M.L. Kawasaki: A. Leaves and inflorescences. B. Flower bud. C. Medial section of ovary. D. Cross section of ovary. E. Fruit. F. Digital scan of flower buds. (A–C,** ***Palacios 6723*****; D–F,** ***Quizhpe et al. 145*****).**

trichomes grow in a different direction, possibly where bracteoles lobe rests), the margin more or less entire; petals cream color (live) with plentiful glandular dots, ciliate, rounded eliptical, 16–21 × 11–12 mm, the tip more or less obtuse; stamens numerous (approaching 100), the anthers ca. 1 mm long, the filaments 17–20 mm long. **Fruits** berries resembling drupes, oblong, 13–28 × 8–16 mm, the hairs clustered in groups, black at maturity; seed 1, mature size unknown, the seed coat membranous; embryo eugenioid, the cotyledons fleshy, connate, the radicle indistinct.

Distribution.—Known only from Carchi province (Reserva Etnica Awá), in primary rain forests and premontane forests at 650–1800 m elevation.

Eugenia grossa is characterized by the very large leaves (27–45 × 19–25 cm), brown to yellowish brown-

pubescent and large flower buds (ca. 13 mm long), with connate, deciduous bracteoles. Tipaz et al. (*1370*) describe the fruit as "edible" and note the wood is used to make tool handles and walking canes.

Additional collections examined: **ECUADOR. Carchi:** Maldonado, Parroquia Tobar Donoso, Reserva Etnica Awá, Sector Sabalera, 900 m, 00°55'N, 78°32'W, 22 Nov 1992 (fr), *C. Aulestia et al. 830* (MO, QCNE, SEL); Tulcan, Parroquia Tobar Donoso, Reserva Etnica Awá, Centro El Baboso, 1800 m, 00°53'N, 78°25'W, 17–27 Aug 1992 (fr), *C. Aulestia et al. 1817* (MO, QCNE, SEL).

Myrcia subcordifolia B. Holst & M.L. Kawasaki, sp. nov. (**Fig. 4**). TYPE: ECUADOR. ZAMORA-CHINCHIPE: Nangaritza Cantón, valley of Río Nangaritza, Miazi, 04°18'S, 78°40'W, 1200 m, 10 Dec 1990 (fl), *W. Palacios 6723* (HOLOTYPE: QCNE; ISOTYPES: F, MO, SEL).

Arbor; foliis suborbicularis usque ellipticis, coriaceis, glabris, saepe subcordatis; paniculis multifloris; alabastris 2–3 mm longis.

Tree 4–10 m tall, mostly glabrous, the few trichomes on inflorescences and flowers yellowish to yellowish white. **Leaf blades** suborbicular to elliptic, or ovate, 4–9.5 × 3–6 cm, coriaceous, plane, glabrous, drying dark brown to brownish above, paler below; apex obtuse to rounded; base rounded or broadly subcordate; midvein impressed above, convex below; lateral veins 7–10 pairs, slightly convex on both surfaces; marginal veins 2, the innermost 1–2 mm from blade margin, similar to the lateral veins; glands numerous, punctiform, indistinct or impressed above, salient below; petiole 1–3 mm long, channeled, puberulous to glabrous, black. **Inflorescences** paniculate, subterminal, multiflorous (approx. 20–60 flowers), 6–12 cm long, puberulous; bracts and bracteoles not seen, early deciduous. **Flowers** 5-merous, buds obovoid to subglobose, 2–3 mm long; calyx-lobes suborbicular, to 1 mm long, appressed-pubescent to puberulous without, glabrous within; petals suborbicular, ca. 2 mm diam.; stamens numerous, the filaments ca. 4–5 mm long, the anthers ca. 0.5 mm long; style ca. 5 mm long, the stigma punctiform; hypanthium not prolonged beyond the ovary, sericeous without; disk ca. 2 mm diam., hirsutulous; ovary 2-locular, 2 ovules per locule. **Fruits** (immature) berries, ellipsoid, ca. 5 mm long, glabrous; seeds not seen.

Distribution.—This species is known from Zamora-Chinchipe and Morona-Santiago, in the Cordillera del Cóndor region; it occurs in primary, premontane wet forests, at 900–1200 m elevation.

Myrcia subcordifolia resembles *Myrcia clusiifolia* (Kunth) DC., a species known from lowland, white-sand savannas from Venezuela, Colombia, and Amazonian Brazil (Holst et al., 2003). In *M. subcordifolia*, however, the leaves are subsessile with petioles 1–3 mm long and plane (vs. petiolate with petioles 5–8 mm long, and the leaves convex-conduplicate), the lateral veins are slightly convex, and the veinlets are indistinct (vs. veins strongly convex and veinlets distinctly reticulate) on both surfaces.

Additional collections examined: **ECUADOR. Morona-Santiago:** Limon Indanza, Cordillera del Cóndor, Centro Shuar Yunkumas, Asociación Nunkui, Cerro Chuank Naint, 03°03'34"S, 78°14'45"W, 1150 m, 19 Dec 2005 (fl), *C. Morales et al. 1595* (F, MO, QCNE). **Zamora-Chinchipe:** Nangaritza, region of Cordillera del Cóndor, upper river basin of Río Nangaritza, Sector Las Orquídeas, W of river, 04°12'22"S, 78°39'16"W, 1100 m, 7 Aug 2002 (fl, yfr), *W. Quizhpe et al. 145* (F, MO, SEL); Nangaritza, region of Cordillera del Cóndor, 900 m, 04°17'10"S, 78°38'50"W, 24 Jul 2003 (fl), *W. Quizhpe et al. 638* (MO, SEL); El Pangui, Cordillera del Cóndor, W slopes, Machinaza river basin, 03°37'31"S, 78°31'50"W, 1050 m, 22 Mar 2006 (fl), *W. Quizhpe & F. Luisier 2043* (F, LOJA, MO).

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We thank the herbaria cited in the manuscript for providing the collections used in this study. Fred Barrie offered helpful suggestions to improve the manuscript. Illustrations are by Valerie Renard and Lucia Kawasaki.

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BOOK REVIEW

Glafiro Alanís Flores. 2007. **El Valor de Nuestras Plantas.** (ISBN 978-970-9715-26-2, hbk.). Fondo Editorial de Nuevo León, Zaragoza 1300, Edificio Kalos, Nivel A2, Desp. 249, CP 64000, Monterrey, Nuevo León, Mexico. (**Orders:** www.fondoeditorialnl.gob.mx, (81) 8344 2970 y 71). $150.00, 157 pp., color photographs, b/w line drawings, color paintings, 9" × 9".

Contents:

Presentación
Nuestras plantas
Leyenda del ánima anacahuita
¿Por qué comemos mahuacatas?
La inundación de 1909
El sabino gordo de Terán
La dominante gobernadora
La deliciosa nieve de pitaya
El preciado oro verde
Cómo plantar un árbol

This is a delightfully charming book filled to the brim with school children's paintings of northeastern Mexican flowers and plants. This compilation comes from students in 58 ecological clubs around the state of Nuevo León, Mexico, who have studied native plants and learned how to draw them. While acknowledging the practical services provided by plants, such as global climate control and sustenance, the book communicates the aesthetic value of plants and the importance of training a new generation to take up a commitment to conservation. Education is promoted as a means to incite Nuevo León to protect the natural areas that still remain in its municipalities, to responsibly reforest with native species, and to encourage further research into new ways to use plants. Loving and at times quite masterful illustrations grace the approximately 30 plant species that are described, along with comments on their local distribution, methods and requirements for their propagation, and their current and potential uses. Interspersed throughout the illustrations are narratives espousing the values of nature, quoted from figures important to the history of Nuevo León. This enchanting call to the conservation of nature will please any reader and stands as a testament to the value of an environmental education and a meeting point between the arts and sciences.—*Tiana Franklin, Botanical Research Institute of Texas, 500 East 4th Street, Fort Worth, Texas 76102-4025, U.S.A.*

CLARIFICATION OF *BORRERIA GYMNOCEPHALA*, *DIODIA GYMNOCEPHALA*, *DIODIA SCHUMANNII*, *BORRERIA FLAVOVIRENS*, AND *SPERMACOCE SCHUMANNII* (RUBIACEAE)

Piero G. Delprete

Federal University of Goiás, Campus II
Institute of Biological Sciences - ICB-1
Department of General Biology/Botany
74001-970 Goiânia, Goiás, BRAZIL
pdelprete@hotmail.com

Joseph H. Kirkbride, Jr.

USDA-ARS, U.S. National Arboretum
Floral & Nursery Plants Research Unit
Washington, DC 20002-1958, U.S.A.
joseph.kirkbride@ars.usda.gov

ABSTRACT

Several erroneous, confused, and/or misapplied names, e.g., *Borreria gymnocephala*, *Diodia gymnocephala* and *Diodia schumannii*, have been variably assigned to the same species by many authors. The status of all these names is here clarified, and the correct name for the species involved is established as *Spermacoce schumannii* (Standl. ex Bacigalupo) Delprete.

Key Words: *Borreria*, *Spermacoce*, Rubiaceae, Goiás, Tocantins, Brazil, Argentina, Neotropics

RESUMEN

Vários nomes errados, confusos e/ou não corretamente aplicados, e.g., *Borreria gymnocephala*, *Diodia gymnocephala* e *Diodia schumannii*, foram variavelmente usados para a mesma espécie por muitos autores. A saga de todo estes nomes é aqui clarificada e o nome certo desta espécie foi estabelecido de ser *Spermacoce schumannii* (Standl. ex Bacigalupo) Delprete.

Palavras Chave: *Borreria*, *Spermacoce*. Rubiaceae, Goiás, Tocantins, Brasil, Argentina, Neotrópicos

INTRODUCTION

The present work seeks to clarify the status of the incorrect, confused, and/or misapplied names [e.g., *Borreria flavovirens* Bacigalupo & E.L. Cabral, *Borreria gymnocephala* DC., *Diodia gymnocephala* (DC.) K. Schum., *Diodia schumannii* Standl. ex Bacigalupo] of taxa related to *Spermacoce schumannii* (Standl. ex Bacigalupo) Delprete (Rubiaceae, Spermacoceae).

Candolle (1830, p. 549) described *Borreria? gymnocephala* DC., and was uncertain about its generic position. He cited a specimen in his herbarium without giving the collector or the specific collection locality. After the description he stated that this species, collected in Brazil, is so distinct that it could even be treated as a separate genus and is characterized by 4-angular, smooth stems between the capitate inflorescences and small corollas with included anthers.

Schumann (1888) transferred Candolle's taxon to the genus *Diodia* as *D. gymnocephala* (DC.) K. Schum. After the description, he stated that it is very similar to *Borreria latifolia* (Aubl.) K. Schum. var. *siderites* (Cham. & Schltdl.) K. Schum., from which it differed by the yellowish color of the vegetative parts and the fruit and style morphology. However, both Schumann's description and the specimens he cited apply to a mixture of two species.

According to Bacigalupo and Cabral (1998), Standley was the first to notice that Schumann's *Diodia gymnocephala* encompassed two distinct species. He annotated some herbarium specimens, which belonged to the part of *D. gymnocephala* that differed from Candolle's *Borreria gymnocephala*, as *Borreria schumannii* Standl. Bacigalupo (1974) treated this same species in volume 6, part 6 of the *Flora Ilustrada de Entre Ríos (Argentina)*, and published Standley's name as "*Diodia schumannii* Standley ex Bacigalupo, nov. nom." with Schumann's *D. gymnocephala* listed as a synonym and Candolle's *B. gymnocephala* specifically excluded. Article 69 of the ICBN (Stafleu et al. 1972) in force at that time stated that "A name is to be rejected if it is used in different senses and so has become a long-persistent source of error." Whether Bacigalupo intended to completely

reject *D. gymnocephala* (DC.) K. Schum. or was simply creating a new name for *D. gymnocephala* sensu K. Schum. is not entirely clear in this *Flora*, since no further discussion of nomenclature was provided.

Since the type of *D. gymnocephala*, i.e. *Borreria gymnocephala* DC., was explicitly excluded by Bacigalupo (1974), the citation of this earlier name does not make *D. schumannii* illegitimate under current ICBN Art. 52 (McNeill et al. 2006). But, apart from having the correct Latin form, does this name meet the other requirements under Art. 32.1 for valid publication, namely provision of a Latin description or diagnosis (since 1935) and indication of a type (since 1958)? Bacigalupo (1974) provided only a Spanish description, but her reference to Schumann's name, for which a full Latin description was provided, is an acceptable "reference to a previously and effectively published Latin description" under Art. 36. In addition, under this species Bacigalupo cited only the single specimen "Dpto. La Paz, isla Curuzú Chalí, Burkart 27.103 (SI)." When Bacigalupo (1974) published her new species, Art. 37 of the ICBN (Stafleu et al. 1972), then in effect, stated: "Publication on or after 1 Jan. 1958 of the name of a new taxon of the rank of family or below is valid only when the nomenclatural type is indicated ..." thus her citation would not then have satisfied this requirement and her new name was not validly published under the 1972 Code.

It was this fact that motivated Bacigalupo and Cabral (1998) to later propose a new name, *B. flavovirens* Bacigalupo & E.L. Cabral, to replace *Diodia schumannii* Standley ex Bacigalupo, "nom. illeg.", which had been published "sin seleccionar el tipo", although in reality this shortcoming would have affected its valid publication and not its illegitimacy. However, these authors had overlooked the fact that already in the 1988 ICBN (Greuter et al. 1988) Art. 37 had been expanded considerably to include, in Art. 37.3, the following: "for the name of a new species or infraspecific taxon, citation of a single element is acceptable as indication of the holotype." In the current ICBN (McNeill et al. 2006) this is now stated as: "for the name of a new species or infraspecific taxon, mention of a single element or gathering ..., even if that element is not explicitly designated as type, is acceptable as indication of the type." Since Bacigalupo's (1974) citation of a single specimen fulfills the requirement for a type indication, *D. schumannii* has been validly published under all editions of the ICBN since 1988. Thus *B. flavovirens* was at the outset a nomenclaturally superfluous and illegitimate replacement name for *D. schumannii*.

In their 1998 paper, Bacigalupo and Cabral finally clarified the status of *Diodia gymnocephala* (DC.) K. Schum., which from their examination of the type of the basionym, *B. gymnocephala* DC. (1830), at G-DC they determined to be synonymous with *Borreria palustris* (Cham. & Schltdl.) Bacigalupo & E.L. Cabral, this based on the earlier *Diodia palustris* Cham. & Schltdl. (1828).

A further point should be made with regard to the type of *Diodia schumannii* Standley ex Bacigalupo. Because this name was "validly published by reference to a previously and effectively published description or diagnosis," that of Schumann (1888) as has already been noted, Art. 7.7 dictates that it "is to be typified by an element selected from the context of the validating description or diagnosis, unless the validating author has definitely designated a different type." While Bacigalupo can be said to have satisfied the Art. 37 requirement for "indication" of a type, according to Art. 7.11 "designation" of a type requires the inclusion of "the term 'type' or an equivalent." So unless the term "Exsiccata" used by Bacigalupo is considered equivalent to "type," which seems unlikely, does this mean that the indication of type under Art. 37 does not qualify as designation of a different type under Art. 7.7, such that *D. schumannii* must be typified on an element cited by Schumann? It is our interpretation that in this case an "indication" in the one case is equivalent to a "designation" in the other, such that the type of *D. schumannii* is that indicated by Bacigalupo in 1974.

In conclusion, the species discussed above is maintained within the genus *Spermacoce*, as *S. schumannii* (Standl. ex Bacigalupo) Delprete, following the circumscription adopted by Delprete et al. (2005), Delprete and Cortés-B. ("2006" [2007]), and Delprete (2007).

SYSTEMATIC TREATMENT

Spermacoce schumannii (Standl. ex Bacigalupo) Delprete in A. Reis, Fl. Ilustr. Catarin. RUBI 2:754, fig. 130. 2005. *Diodia schumannii* Standl. ex Bacigalupo in A. Burkart, Fl. Ilustr. Entre Ríos 6(6):15, fig. 5. 1974. *Borreria flavovirens* Bacigalupo & E.L. Cabral, Hickenia 2: 261, fig. 1. 1998, nom. illeg. Type: ARGENTINA. Entre Rios: Dpto. La Paz, Isla Curuzú-Chalí, 10 Apr 1968 (fl, fr), *Burkart et al. 27103* (holotype: SI n.v.; isotype: CTES n.v.; photos-CTES at NY!, UFG!).

Diodia gymnocephala sensu K. Schum. in Mart., Fl. Bras. 6(6):16. 1888, p.p.; non *Borreria gymnocephala* DC., Prodr. 4:549. 1830 [= *Spermacoce palustris* (Cham. & Schltdl.) Delprete]

Selected specimens examined: **BRAZIL: Goiás:** Serra do Caiapó, ca. 30 km (straight line), S of Caiapônia, 950–1200 m, 29 Apr 1973 (fl, fr), *Anderson et al. 9363* (NY, UB); Serra Dourada, 16°3'S, 50°7'W, 920 m, 17 Mar 1989 (fl, fr), *Cavalcanti et al. 461* (CEN, NY[2]); Mun. Alto Paraíso, Chapada dos Veadeiros, 10 km W of Alto Paraíso, 1000 m, 24 Mar 1969 (fl), *Irwin et al. 24971* (NY, UB); Mun. Mossâmendes, Serra Dourada, ca. 6 km NE of Mossâmendes, 16°04'S, 50°11'W, 1000 m, 7 Feb 1980 (fl), *Kirkbride 3293* (NY, UB); Mun. Niquelândia, estrada Go-237 entre Niquelândia e Colinas, 14°21'S, 48°12'W, 470 m, 13 Apr 1992 (fl, fr), *Walter et al. 1226* (CEN, NY). **Mato Grosso:** Ca. 35 km (straight line) ENE of Barra do Garças, 500 m, 4 May 1973 (fl, fr), *Anderson et al. 9688* (NY, UB); roadside from base camp to main Xavantina-Cachimbo rd., km 264, 16 Nov 1967 (fl), *Philcox et al. 3068* (NY). **Minas Gerais:** Serra do Espinhaço, ca. 15 km NE of Diamantina, on rd to Mendanha, 1300 m, 26 Jan 1969 (fl), *Irwin et al. 22605* (NY); Mun. Formoso, Parque Nacional Grande Sertão Veredas, towards Faz. Diamante, 15°20'01"S, 45°56'54"W, 815 m, 29 Nov 1997 (fl), *R.C. Mendonça et al. 3308* (IBGE, NY); Mun. Diamantina, Fundo do Macaco, 1200 m, 16 May 1931 (fl, fr), *Mexia 5849* (NY). **Paraná:** Mun. Morretes, Estr. da Graciosa, Alto da Serra, 12 Feb 1965 (fl), *Hatschbach 12367* (US). **Rio de Janeiro:** Mun. Caxias, Capivarí, 30 Sep 1958 (fl), *E. Pereira 4212* (HBR); Mun. Jacarepaguá, Restinga de Jacarepaguá, 10 Sep 1958 (fl), *E. Pereira 4159* (HBR, NY). **Santa Catarina:** Mun. Lages, Alto da Serra, Encruzilhada, mata secundária, 900 m, 7 Nov 1946 (fl), *Reitz & Klein 12571* (HBR, NY); Mun. Lauro Müller, rd. SC-403, km 12, Novo Horizonte, property of Olavo Mariotti, 28°23'S, 49°28'W, 420 m, 5 Dec 1998 (fl), *Delprete et al. 6986* (HBR, MBM, MO, NY, UB, US). **São Paulo:** Mun. Atibaia, 0.5 km N of Atibaia, 24 Sep 1960 (fl), *Mattos & Mattos 8389* (NY); São Paulo, Avenida Paulista, campo, Oct 1913, *Brade 6803* (NY). **Tocantins:** Mun. Couto de Magalhães, rd. Couto de Magalhães-Colinas de Tocantins (TO-335), 5–8 km from Couto de Magalhães, 170–200 m, 08°19'29"S, 49°09'25"W, 4 Nov 2005 (fl, fr), *Delprete et al. 9267* (NY, UB, UFG); Mun. Araguaína, 15 km S of Araguaína, 300 m, 15 Mar 1968 (fl), *Irwin et al. 21199* (UB).

Distribution and ecology.—Widespread from Colombia to southern Brazil, Paraguay, and northern Argentina. In Brazil, it is known from the states of Rondonia, Mato Grosso, Goiás, Tocantins, Minas Gerais, Maranhão, Bahia, and southwards throughout Rio Grande do Sul. Mostly found at the margins of and inside gallery forests, semi-deciduous forests, and slope forests, and less frequently in seasonally flooded vegetation.

Taxonomic observations.—*Spermacoce schumannii* is very similar to *S. latifolia* Aubl. in its flexuous, somewhat climbing habit, and floral branches with 5–13 glomerules, but it differs in its cylindrical to cupular, 3–8 mm long stipular sheath [vs. short, triangular, (1–)2–5 mm long in *S. latifolia*] and commonly yellowish tinge of the vegetative parts (vs. pale to olive green).

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ARISTIDAE ELUDENDAE II: A RE-EVALUATION OF THE *ARISTIDA GIBBOSA* COMPLEX (POACEAE: ARISTIDEAE), INCLUDING *A. MARGINALIS*, *A. ORIZABENSIS*, AND *A. SORZOGONENSIS*

Robert T. Strahan and Kelly W. Allred

Range Science Herbarium
Department of Animal & Range Sciences
New Mexico State University
Las Cruces, New Mexico 88003, U.S.A.
rstrahan@nmsu.edu; kallred@nmsu.edu

ABSTRACT

Taxonomic relationships based on morphological variation among *Aristida gibbosa*, *Aristida marginalis*, *Aristida orizabensis*, and *Aristida sorzogonensis* were assessed by principal component analysis. Results of the PCA indicate two distinct clusters corresponding to *A. gibbosa* and *A. sorzogonensis*. The two taxa are distinguished by a number of vegetative and spikelet features. Within *A. sorzogonensis*, two taxa are recognized at the *forma* level based on pulvini development. *Aristida marginalis* was represented by a single specimen (the type) that was isolated between the *A. gibbosa* and *A. sorzogonensis* clusters. **Aristida sorzogonensis** f.**orizabensis** (E. Fourn.) Strahan & Allred is a new combination. A key to determine the species of the *Aristida gibbosa* complex, brief descriptions, and specimens examined are provided.

RESUMEN

Las relaciones taxonómicas basadas en variaciones morfológicas entre *Aristida gibbosa*, *A. marginalis*, *A. orizabensis*, y *A. sorzogonensis* se evaluaron empleando el Análisis de Componentes Principales (PCA). Los resultados de éste análisis indican que existen dos grupos distintos caracterizados por *A. gibbosa* y *A. sorzogonensis*. Las diferencias entre estas dos especies o grupos incluyen características vegetativas y también diferencias entre espiguillas. Dentro del grupo correspondiente a *A. sorzogonensis*, se reconocen dos taxa a nivel "forma" basados en el desarrollo de los pulvínulos. *Aristida marginalis* está representada por una sola colección (Typus) y se ubicó en forma aislada entre los grupos de *A. gibbosa* y *A. sorzogonensis*. ***Aristida sorzogonensis*** f. ***orizabensis*** (E. Fourn.) Strahan & Allred, es una nueva combinación. Se incluye una clave para determinar las especies del complejo *Aristida gibbosa*, descripciones breves y los especímenes examinados.

INTRODUCTION

The genus *Aristida* L. comprises some 250–350 species, nearly worldwide in distribution, growing in warmer, more arid environments (Allred 2003). Members are characterized by a panicle inflorescence, one-flowered spikelets, and relatively large glumes, usually larger than the floret. The florets are characterized by three awns, the two lateral awns absent or much reduced in some species, and a sharp pointed callus with a tuft of hair at the base. In some cases the lemma body is drawn out into an elongated beak below the divergence of the awns. The genus has its share of taxonomically difficult species complexes. Members of such groups often differ only slightly morphologically and commonly overlap in their geographic distribution (Allred 1984a, 1984b; Longhi-Wagner 1990).

The *Aristida gibbosa* complex is one such group. This New World complex is characterized by the following two features: 1) floret sulcate, the margins of the lemma slightly overlapping, and 2) callus short, 0.3–0.4 mm long, the attachment scar circular and tiny, 0.2–0.3 mm in diameter (Fig. 1). New World taxa corresponding to these features have received the following names (in chronological order):

Chaetaria gibbosa Nees (1829): In his ample description, Nees noted the regular branching of the culms, short lower sheaths exposing the gibbous nodes (whence the specific epithet), and folded or rolled leaf blades. Blade margins are not thickened, the marginal veins being no wider than those inward, and the adaxial surface is lacking pilose hairs except at the corners of the sheath. Panicles lack pulvini and are thus narrow and contracted. This is a South American species, and the name was unused in North and Central American works until Longhi-Wagner (1990) called attention to the sulcate lemma of numerous specimens

at MO and US and annotated them as this. The name was then applied, in an expanded sense, to Meso-American plants by Pohl and Davidse (1994) to include *Aristida sorzogonensis, A. orizabensis,* and *A. marginalis.*

Fig. 1. Sulcate lemma with tiny circular attachment scar (arrow).

Aristida sorzogonensis J. Presl (1830): Erroneously believing Haenke's specimen to be from Sorsogon on the island of Luzon in the Philippines, Presl applied the specific epithet *sorzogonensis* to his new species. It is highly probable that the specimen actually came from Central America or Mexico (annotation in 1921 on the type by E.D. Merrill; Henrard 1928). The type collection is represented by at least two sheets, both with a single flowering culm: the holotype at PR(!) has three mid- to upper blades, but lacks the base of the plant or any basal blades; an apparent isotype at PR(!) has a culm with three upper blades and two mid- to lower blades. Presl described the blades as convolute-setaceous, which the upper are, but the middle and lower blades are flat (perhaps rolled a bit upon drying) in both specimens. Blade margins are noticeably thickened, with a wide band of sclerenchyma at the margin; this is easily visible even on the upper blades that are rolled. The adaxial surface has prominent pilose hairs upwards from the throat region. A close examination of the panicle branches and pedicels reveals small (perhaps young) pulvini in nearly all the axils, with the resultant slight spreading of the axes, a feature not noted for this species in any previous works. The name *Aristida sorzogonensis* has been largely ignored or unknown by nearly all North American botanists, even though Henrard recognized it in both his Revision and Monograph of *Aristida* (Henrard 1929, 1932). Pohl and Davidse (1994) rightly called attention to the priority of *sorzogonensis* over *orizabensis* and *marginalis*, but we believe they misinterpreted the typification in tentatively applying the name *sorzogonensis* to plants with rolled, rather than flat, blades.

Aristida liebmanii E. Fourn. (1886): Fournier's description came from a collection by Liebmann (whence the specific epithet) and noted the following distinctive features: basal blades are flat and the upper blades are rolled (much as in the type of *A. sorzogonensis*), and first glumes are longer than the second. He did not call attention to the nearly complete absence of an elongated beak on the lemma, the awns immediately diverging from the apex, but this was stressed by Henrard (1927), is easily observable in the type, and was re-emphasized by Pohl and Davidse (1994). An isotype at MO(!) contains three flowering shoots and one basal portion. The margins of the blades are noticeably thickened, and the lower panicle branches are naked at the base and somewhat flexuous. Panicles are non-pulvinate. Pohl and Davidse (1994) called attention to its similarity with *A. succedeana* Henr., a species of Bolivia and Brazil that also has sulcate lemmas, flat blades, and sub-flexuous panicle branches, with the suggestion that the two may be conspecific. However, because of the scarcity of specimens further analysis and conclusions concerning this species must await the availability of more material.

Aristida orizabensis E. Fourn. (1886): Fournier's description, though short, mentions flat blades (rolled upon drying), somewhat unequal glumes, and a narrow lemma that was slightly shorter or longer than the glumes. Material came from "Valle de Orizaba," Veracruz, Mexico (whence the specific epithet), with Fournier citing two specimens, which are considered syntypes. Isosyntypes at NY(!) and US(!) have flat, curling blades with thickened margins and with long pilose hairs on the adaxial surface near the ligule, and panicles lacking pulvini. Henrard (1927) contrasted *A. orizabensis* with *A. arizonica* Vasey and *A. appressa* Vasey, two species excluded from this complex that lack sulcate lemmas.

Aristida marginalis Ekman (1911): This species was named from material collected along the dry, grassy edges of forests or woods ("in margine silvulae," whence the specific epithet) in Matto Grosso, southern Brazil. The new species is very well described by Ekman. In type material (isotypes G!, US!), sheaths are about half as long as the numerous internodes with gibbous nodes; lower blades are flat, curling, and thick-margined with pilose adaxial surfaces; the panicle is obscurely and incompletely pulvinate (i.e., with poorly developed pulvini in the axils of some branchlets and pedicels); and the lemmas are sulcate with a

short, circular callus. Longhi-Wagner (1990) subsumed this name under *A. gibbosa*, using comparisons of spikelet features such as beak length and relative glume length. The name *A. marginalis* has been applied to numerous Mexican specimens with flat, curling blades and well-developed pulvini.

This study investigates the relationships among *Aristida gibbosa, A. sorzogonensis, A. orizabensis,* and *A. marginalis* using multivariate analysis of morphological characters scored from herbarium specimens to assess species boundaries and determine the usefulness of certain traits used to distinguish them.

MATERIALS AND METHODS

For analysis of taxonomic relationships, specimens identified as *Aristida gibbosa, A. sorzogonensis, A. orizabensis,* and *A. marginalis* were obtained from the following herbaria: F, G, MO, NMCR, US, and WIS. All specimens were examined for a sulcate lemma to distinguish them as members of the *A. gibbosa* complex. A complete examination of all specimens yielded 90 OTUs (operational taxonomic units) for the analysis, including type specimens of *A. gibbosa, A. sorzogonensis, A. orizabensis,* and *A. marginalis*. The specimens used represented the full geographic distribution of the species complex from northern Mexico through Central and South America. A complete data set is available upon request. Roughly two-thirds of the specimens received that were identified in herbaria as *A. orizabensis* were actually *A. appressa*, and not included in this study. In addition to not having a sulcate lemma, *A. appressa* develops a thicker beak (0.2–0.3 mm), usually longer lemma (7–16 mm), and longer callus (0.6–1 mm) with a longer, elongated (rather than circular) attachment scar.

Each OTU was scored for 13 characters, seven discrete and six continuous (Table 1). All discrete characters were recorded for mature vegetative features as present or absent, with and without the aid of a dissecting microscope depending on the nature of the character. All spikelet measurements were taken using an ocular micrometer on a dissecting microscope and were obtained from one mature spikelet from each specimen. Panicle measurements were taken using a standard metric ruler. Principal components analysis (PCA) of the standardized data was conducted using Kovach (2005).

RESULTS AND DISCUSSION

An initial PCA of all OTUs indicated morphological differences with 83% of the variability among specimens occurring along the first three components (Table 2). This is due in part to high variable-to-variable correlations among various discrete features of leaf blade pubescence, type of blade involution and curling, thickness of margins, and shape of nodes (Table 3); the high correlations render these features taxonomically important.

Component I accounted for 60.1% of the variability among OTUs, mostly reflecting weak correlations of vegetative features. Component II accounted for 14.9% of the variability, correlating variation in awn and glume lengths, and Component III correlated with pulvini and panicle length (Table 2).

Dispersion of OTUs was greatest along the first two components, with resolution between two morphologic groups occurring along component I (Fig. 2). The two groups were distinguished by a combination of vegetative and spikelet features. OTUs corresponding to Group 1 are characterized by leaf blades folded and straight (Fig. 3), gibbous nodes (Fig. 4), lacking pilose hairs on the adaxial surface, margins not thickened (Fig. 5), smaller glumes, shorter awns, and shorter callus to awn lengths (Figs. 6–7). OTUs clustered in Group 2 are characterized by contrasting features: curling leaf blades (Fig. 8), terete nodes (Fig. 9), leaf blades flat with thickened margins and prominent pilose hairs on the adaxial surface (Fig. 10), larger glumes, longer awns, and longer callus to awn lengths (Figs. 11–12). The type of *Aristida gibbosa* fell within Group 1, and the types of *Aristida sorzogonensis* and *A. orizabensis* fell within Group 2. The placement of the type specimen of *A. marginalis* between Groups 1 and 2 is a result of its having some features of Group 1 (gibbous nodes, branching culms) and some features of Group 2 (flat curling blades, adaxial pubescence).

Because members of Group 2 had previously been identified as three different species (*marginalis, orizabensis, sorzogonensis*), as well as including both pulvinate and non-pulvinate panicles, a second PCA

Table 1. Morphological features scored for principal components analysis, showing discrete and continuous features and how each was scored.

Discrete Features	Feature Present = 1	Feature Absent = 0
BRANCHING	culms branched	culms unbranched
NODES	nodes terete	nodes gibbous
CURLING	leaf blades curling	leaf blades straight
INVOLUTION	leaf blades flat	leaf blades folded
MARGINS	margins thickened	margins not thickened
PUBESCENCE	adaxial surface pilose	adaxial surface glabrous
PULVINI	panicle pulvinate	panicle non-pulvinate
Continuous Features	Feature Measurement	
PAN	panicle length (cm)	
G1L	glume 1 length (mm)	
G2L	glume 2 length (mm)	
CALAWNL	length from callus to awn (mm)	
CENTAWNL	central awn length (mm)	
LATAWNL	lateral awn length (mm)	

Table 2. Factor loadings for the first three components of the principle component analysis of all OTUs. Loadings less that ±0.250 have been replaced by zero.

	Component 1	Component 2	Component 3
Blade adaxial pubescence	0.335	0	0
Central awn length	0	0.504	0
Blade curling	0.337	0	0
Culms branching	0	0	0
Glume l1 length	0.263	0.291	-0.372
Glume 2 length	0.262	0	-0.39
Blade involution	0.337	0	0
Lateral awn length	0	0.476	0
Callus to awn length	0.309	0	0
Blade margins	0.337	0	0
Node shape	0.335	0	0
Pulvini	0	0	0.416
Panicle length	0	0.351	0.663
Total	60.1%	14.9%	8.0%

was conducted on all 54 OTUs of Group 2 (Fig. 13). The first three components of the PCA explained 82% of the variability of this second analysis (Table 4). Dispersion of OTUs along component I was a function of variability in awn lengths, glume lengths, and callus to awn length. Component II revealed differences in the central awn, glume two, and panicle lengths, as well as the pulvini development. Component III corresponded to variation in panicle length and pulvini development (Table 4).

Dispersion of Group 2 OTUs reveals no further clear morphological distinctions, nor a clear separation between pulvinate and non-pulvinate forms, in spite of these being visually distinctive. Axillary pulvini cause panicle branches and pedicels to spread outward, giving the panicle a somewhat diffuse appearance, contrasting with the dense contracted appearance of non-pulvinate panicles (Figs. 14–17).

In summary, spikelet features are deceptively similar among the three species analyzed, and may lead one to consider them as conspecific. In contrast, vegetative features, though often thought to be of lesser value in grass taxonomy, serve very well in distinguishing the species.

TABLE 3. Similarity matrix showing variable by variable correlations for PCA of all OTUs.

	PUBESCENCE	CENTAWNL	CURLING	BRANCHING	G1L	G2L	INVOLUTION	LATAWNL	CALAWNL	MARGINS	NODES	PULVINI	PAN
PUBESCENCE	1.000												
CENTAWNL	0.366	1.000											
CURLING	0.977	0.355	1.000										
BRANCHING	-0.654	-0.259	-0.638	1.000									
G1L	0.545	0.577	0.538	-0.373	1.000								
G2L	0.577	0.484	0.565	-0.370	0.909	1.000							
INVOLUTION	0.977	0.355	1.000	-0.638	0.538	0.565	1.000						
LATAWNL	0.381	0.897	0.380	-0.244	0.582	0.510	0.380	1.000					
CALAWNL	0.732	0.548	0.739	-0.574	0.723	0.725	0.739	0.554	1.000				
MARGINS	0.977	0.355	1.000	-0.638	0.538	0.565	1.000	0.380	0.739	1.000			
NODES	0.954	0.342	0.977	-0.676	0.541	0.565	0.977	0.372	0.756	0.977	1.000		
PULVINI	0.589	0.364	0.603	-0.390	0.372	0.283	0.603	0.346	0.435	0.603	0.594	1.000	
PAN	0.100	0.361	0.066	0.118	0.122	0.149	0.066	0.251	0.133	0.066	0.076	0.191	1.000

TAXONOMIC TREATMENT

Consequent to the results of the PCA, three species are recognized (in addition to *A. liebmannii*, which was not analyzed in this study): *Aristida gibbosa* (Group 1 OTUs), *Aristida sorzogonensis* (Group 2 OTUs), and *Aristida marginalis* (represented solely by the type specimen). Variation in features is described in Table 5.

The recognition of *Aristida marginalis* (based on the two isotypes from a single collection) is problematic, since so little is known about it. It is distinguished from the other two species by a suite of peculiar vegetative features: taller, more robust culms with numerous nodes and conspicuously short sheaths, about half as long as the internodes, exposing the many gibbous nodes. Other features are a mix of *A. gibbosa* and *A. sorzogonensis*: flat, curling blades with adaxial pilose hairs characteristic of *A. sorzogonensis*, and gibbous nodes and branching culms characteristic of *A. gibbosa*. We leave the name *A. marginalis* intact until further analyses are possible.

KEY TO THE SPECIES OF THE *ARISTIDA GIBBOSA* COMPLEX

1. Lemma lacking a beak, the awns almost immediately diverging from the not-twisted apex of the lemma body; awns 2–3 cm long __________ **1. A. liebmannii**
1. Lemma with a well developed beak, often twisted prior to the divergence of awns; awns (0.5–)1–2 cm long.
   2. Blades folded or rolled, straight, the margins not thickened, the adaxial surface glabrous __________ **2. A. gibbosa**
   2. Blades flat, curling, the margins thickened, the adaxial surface pilose with long, scattered hairs.
      3. Nodes evidently gibbous, bulging on one side; culms branching above the base, with 7–8 nodes elevated above the base __________ **3. A. marginalis**
      3. Nodes not gibbous, not bulging; culms generally not branching above the base, with 0–4 nodes elevated above the base __________ **4. A. sorzogonensis**

1. Aristida liebmannii E. Fourn., Mexic. pl. 2:78. 1886. Type: MEXICO: Veracruz: Mirador, Apr 1842, *F.M. Leibmann 662* (holotype: C; isotypes: MO!, US-207485, US-991666 (fragm. ex LE), US-1389797).

We have studied only two specimens: the isotype at MO and an additional specimen (*Burch 6143A*) from Honduras. A brief diagnosis follows [Pohl & Davidse (1994) provide a fuller description]: Sheaths glabrous; blades flat (rolled upon drying or at the ends of the blades), with thickened margins; collar and throat glabrous; panicles narrow, elongate, non-pulvinate, but the lower branches somewhat flexuous and naked at the base; glumes inverse, the first 10–12 mm long, the second 8–9 mm long; lemmas involute, sulcate, a beak absent, the awns diverging immediately at the tip of the lemma; awns 2–3 cm long, ± equal in length.

The combination of a sulcate lemma and long awns is immediately distinctive.

Distribution.—Mexico (Veracruz) and Honduras.

2. Aristida gibbosa (Nees) Kunth, Enum. pl. 1:189. 1833. Basionym: *Chaetaria gibbosa* Nees, Agrostologia Brasiliensis, 383. 1829. Type: BRAZIL: in camis agrestivus provinciae piauhianae et Minarum generalium, May, *K.F.P. von Martius 14* (holotype: M; isotypes: LE-TRIN-1286.01,US-865702 fragm. ex M! & photo!).

Aristida gibbosa is characterized by blades that are folded or rolled, stiffly erect, glabrous, and usually lacking thickened margins. The culms regularly branch above the base and have prominently gibbous nodes, with 2–6(–8) nodes elevated above the base. Panicles are narrow and non-pulvinate.

Distribution.—South America: Bolivia, Venezuela, British Guiana, and Brazil (Fig. 18).

Specimens examined. **BOLIVIA. Santa Cruz:** Santa Cruz, Nuflo de Chavez, Serrania San Lorenzo 10km W of San Javier, 17 Apr 1986, *T. Killeen 1979* (US). **BRAZIL. Without State:** No locality, no date *N. Glaziou 20104, 20106* (US). **Bello Horizonte:** campo, 27 Apr 1936, *M. Barret 4521* (US). **Amazonia:** Estrada macapa-Clevelandia, km 50, 31 Aug 1955, *G.A. Black 18544* (US). **Federal District:** 3km W of the Goias-Distrito Federal border along Highway BR-020-030, 9 Apr 1976, *Davidse et al. 12170* (MO). **Goias:** ca. 15 km (straight line) S of Goias Velho, 10 May 1973, *W.R. Anderson 10039* (MO); no locality, no collector, 20 Apr 1898, *22567* (F); rocky hillside with campo and wooded outcrops, ca. 10 km S of Alto do Pariso, 20 Mar 1969, Irwin et al. 24781 (US); ca. 30 km (straight line) S. of Caiaponia, 29 Apr 1973, *W.R. Anderson 9424* (MO); cerrado on rocky slopes, ca. 38 km N of Veadeiros, 16 Mar 1969, *Irwin et al. 24524* (US). **Maranhao:** "Ilha de Balsas" Region, between the Rios Balsas and Parnaiba, 20 Jun 1962, *Eiten et al. 4865* (US). **Mato Grosso:** in cerrado formation on very sandy soil, 4 Jul 1968, *Ratter et al. 2081* (MO). **Minas Gerais:** Sierra do Cipo, 5 Aug 1936, *W.A. Archer 5028* (US); Lagon Santa, serras a 20 km da cidade, 7 Apr 1951, *G.A. Black 11695* (US); Estado de Minas Gerais, 1 Jan 1951, *Pires et al. 2925* (US); Municipio de Sao Goncalo. BR040, km 251, open cerrado, 25 Jul 1984, *Mori et al. 16988* (MO, US). **Roraima:** along Boa Vista-BV 8 road (BR 174) km 76

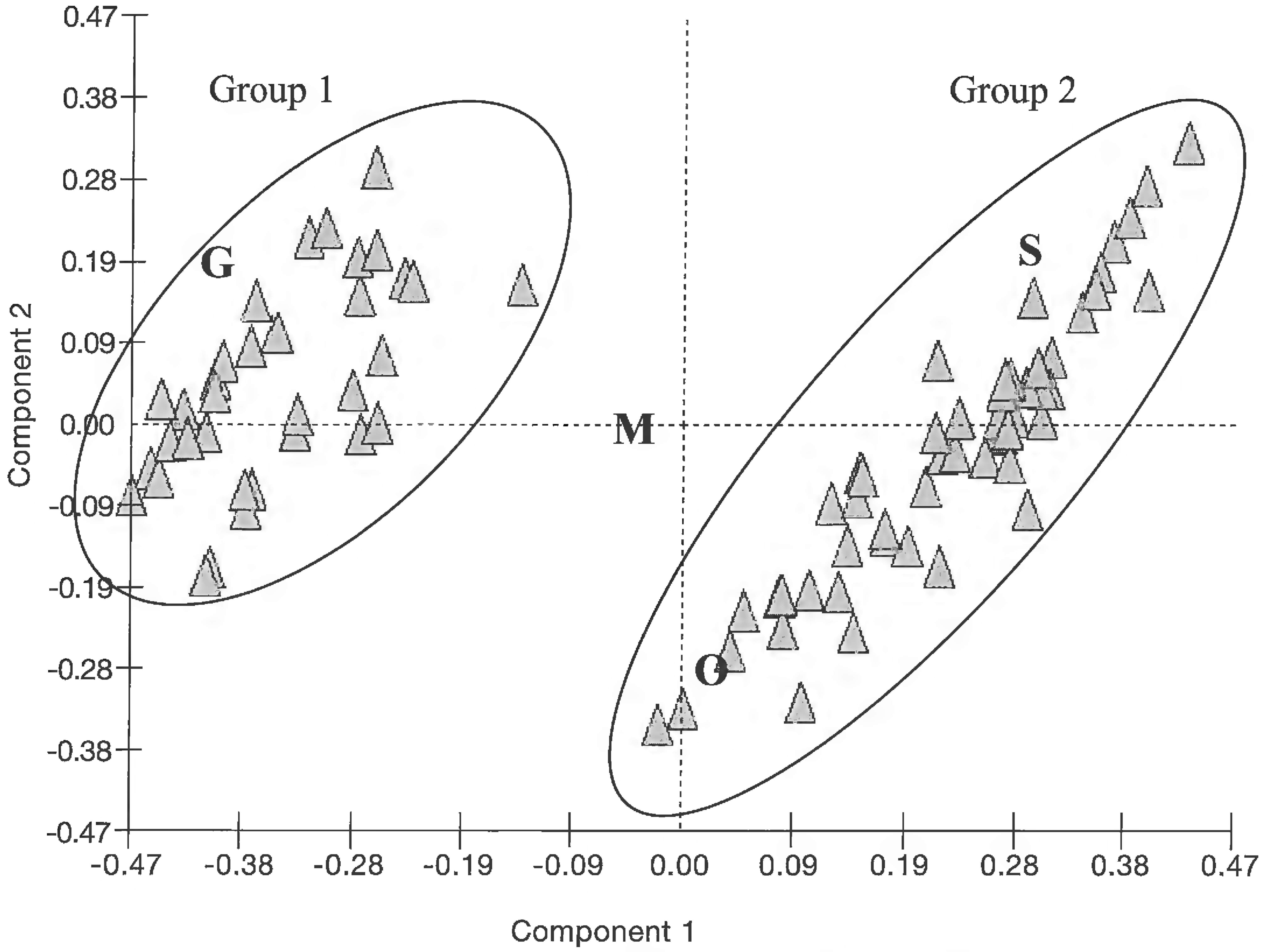


Fig. 2. Dispersion of all OTUs along components I and II of PCA of Aristida gibbosa complex. G = type of *A. gibbosa*. M = type of *A. marginalis*. S = type of *A. sorzogonensis*. O = isosyntype of *A. orizabensis* (*Müller 2103*, US).

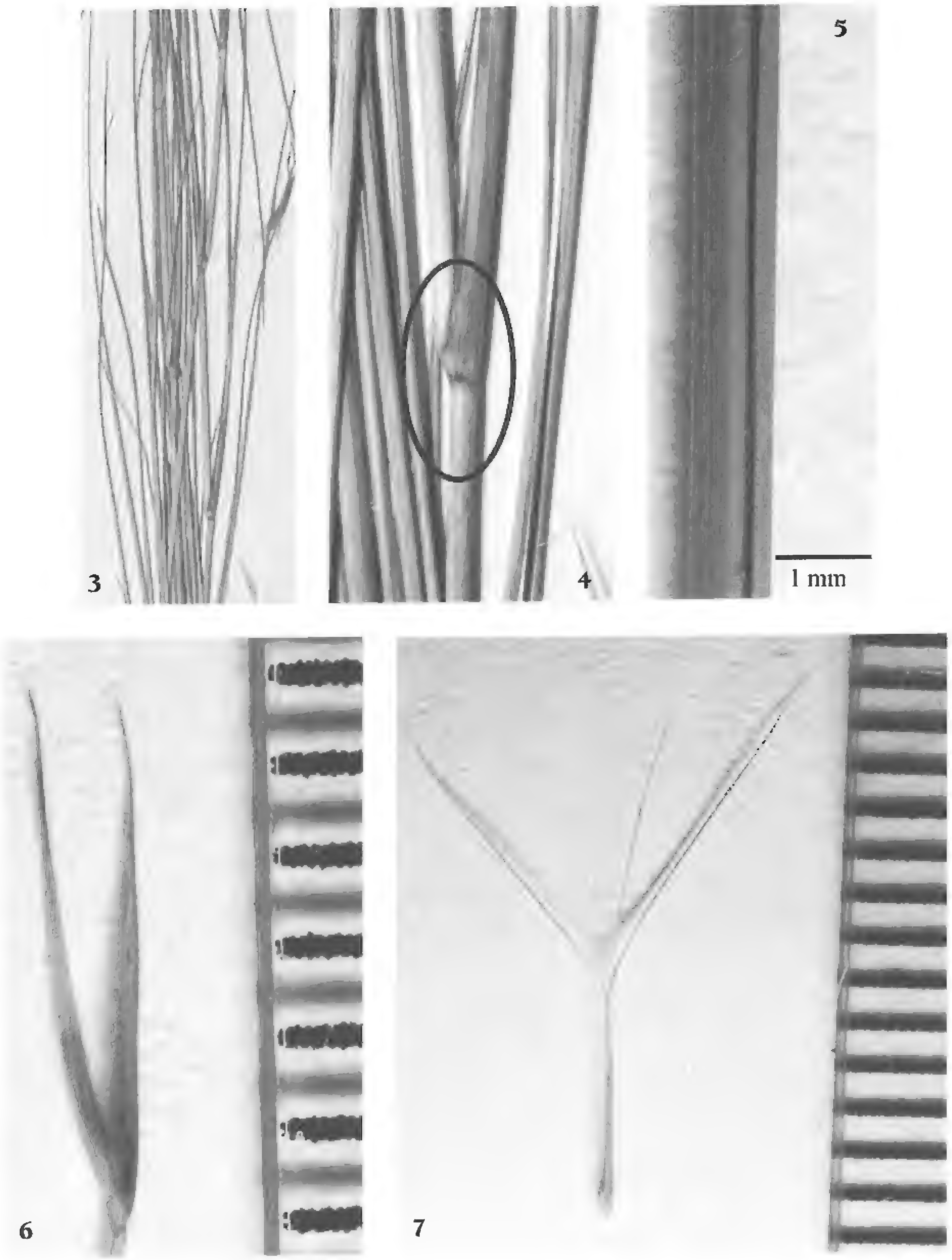
by Uraricoera river, 8 Oct 1977, *Coradin et al. 545* (MO); NE Roraima, ca. 110 km NE of Boa Vista between Bonfim and Guyana border on Tacutu River, 20 Oct 1977, *Coradin et al 792* (US). **BRITISH GUIANA. Rupununi:** no locality 1 Sep 1945, *Fraser, Dr. 378* (US); St. Ignatius dry lateritic ridged savanna 350 ft, 25 Jul 1963, *R. Goodland 22* (US). **VENEZUELA. Anzoategui:** Distrito Bolivar: Rocky mountain savanna, just S of El Zamuro, Fila El Purgatorio, 9 airline km NE of of Bergantin, 24 Nov 1981, *Davidse et al. 19319* (MO). **Aragua:** Carretera Mracay - Choroni, vertiente sur; grama relativemente escasa, en la sabana, 11 Sep 1963, *P. Montaldo 3744* (MO); 12km S of Alto de Choroni (the highest point along the road) on road to Maracay, 14 Nov 1971, *G. Davidse 3068* (MO); 10 km SE of Rancho Grande along road to Maracay, 14 Nov 1971, *Davidse G. 3053* (MO). **Bolivar:** Distrito Piar, middle part of Rio Purpur, affluent of Rio Ambutuir, along trail to Uriman, 30 Nov 1982, *Davidse et 23010* (MO); betweeen Uruyen and Pie de la Roca, SE base of Auyan-tepui, 24 Nov 1982, *Davidse et al. 22559* (MO). **Sucre:** 7 km E of the Mochima Hwy. intersection along Hwy. 9 between Cumana and Puerto La Cruz, 16 Dec 1973, *G. Davidse 5027* (MO).

3. **Aristida marginalis** Ekman, Ark. Bot. 10(17):23, t. 3, f. 2, t. 6, f. 12. 1911. Type: BRAZIL. Matto Grosso: Cuiba, in margine silvulae ('capão') loco sicco, graminoso, arenoso-argilloso, 26 Apr 1903, *G.O. Malme 3143* (holotype S; isotypes G!, US-702283!, US-81202 fragm. ex S!).

Aristida marginalis is known only from the type collection, and is characterized as follows: culms robust, generally about twice as thick as in *A. gibbosa* or *A. sorzogonensis*, branching above the base, with numerous (7–8) nodes elevated above the base; sheaths short, about ½ the length of the internode, straw-colored and contrasting with the pale greenish internode; blades flat, curling, with thickened margins, pilose on the adaxial surface; panicles narrow, but weakly pulvinate.

Distribution.—Known only from Brazil: Matto Grosso, Cuiba (Fig. 18).

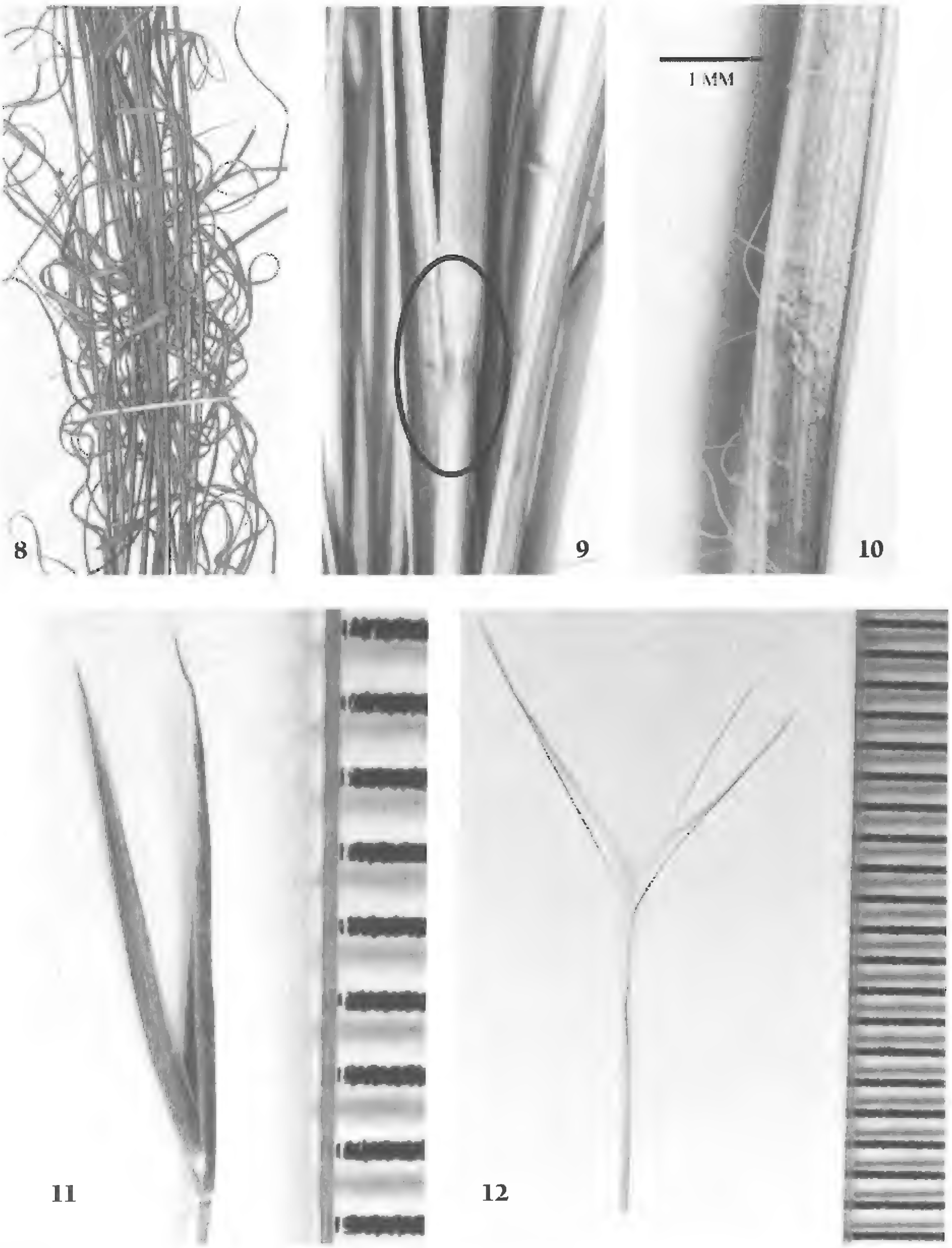
The name *Aristida marginalis* has been applied to similar plants from North America, many of which



Figs. 3–7. 3. Straight leaf blades of Group 1 OTUs. 4. Gibbous nodes of Group 1 OTUs. 5. Folded leaf blade with thin margins and no adaxial pubescence, characteristic of Group 1 OTUs. 6. Glumes of Group 1 OTUs. 7. Floret of Group 1 OTUs. Scales in mm.

are conspicuously pulvinate, particularly collections reported as such by Howard Scott Gentry (1942) from the Rio Mayo region in western Chihuahua. All of these North American plants fall well within the *A. sorzogonensis* cluster on the PCA, and differ from the true Brazilian *A. marginalis* in the features given in the key.

Further field and herbarium work are needed to fully explain the distribution and variation of *Aristida marginalis*. Its apparent intermediacy between *A. gibbosa* and *A. sorzogonensis* seems coincidental, and not a result of hybridization or introgression. As with many species of *Aristida*, species boundaries are likely to be delicate, yet decipherable, and the name should not be discarded as inconsequential.



Figs. 8–12. 8. Curling leaf blades of Group 2 OTUs. **9.** Terete nodes. **10.** Flat leaf blade with thickened margins and prominent pilose hairs on the adaxial surface, characteristic of Group 2 OTUs. **11.** Glumes of Group 2 OTUs. **12.** Floret of Group 2 OTUs. Scales in mm.

4. **Aristida sorzogonensis** J. Presl, in C. Presl, Reliq. haenk. 1(2–4):224. 1830. Type: in Luzonia ad Sorzogon, *T. Haenke s.n.* (holotype: PR photo!; isotypes: LE fragm., PRC photo!, US-81256 fragm. ex W! & photo!, W).

Distribution.—Mostly Mexico and Central America, with a few specimens from northern South America (Fig. 18).

Aristida sorzogonensis is characterized by blades that are flat and curling, with pilose hairs on the adaxial surface and with thickened margins. The culms do not branch above the base and the nodes are not gibbous, with 0–4 nodes elevated above the base. Panicles may be pulvinate or non-pulvinate, which is a minor feature, but the visual differences are immediately noticeable (Figs. 14–17). As has been done

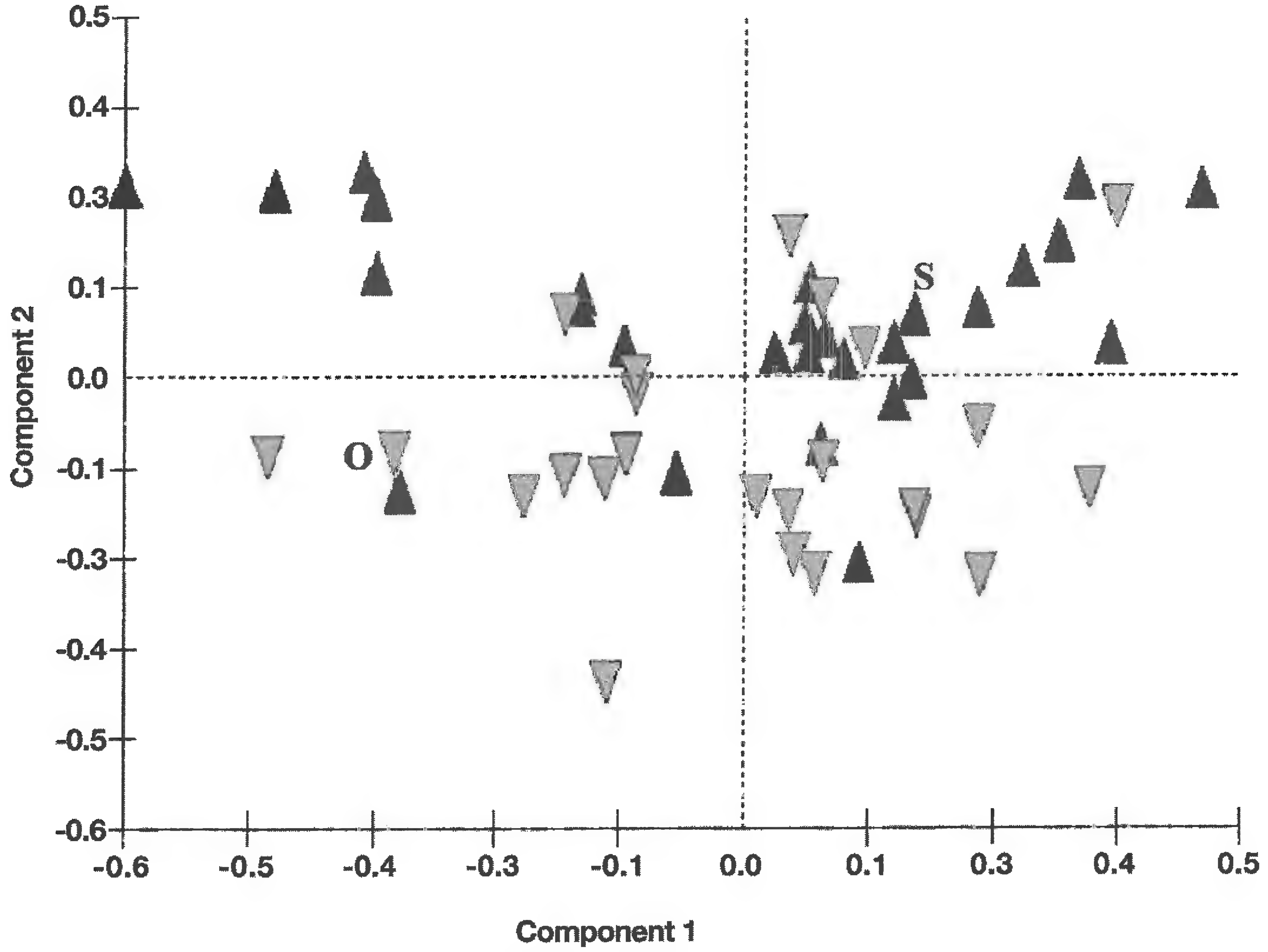
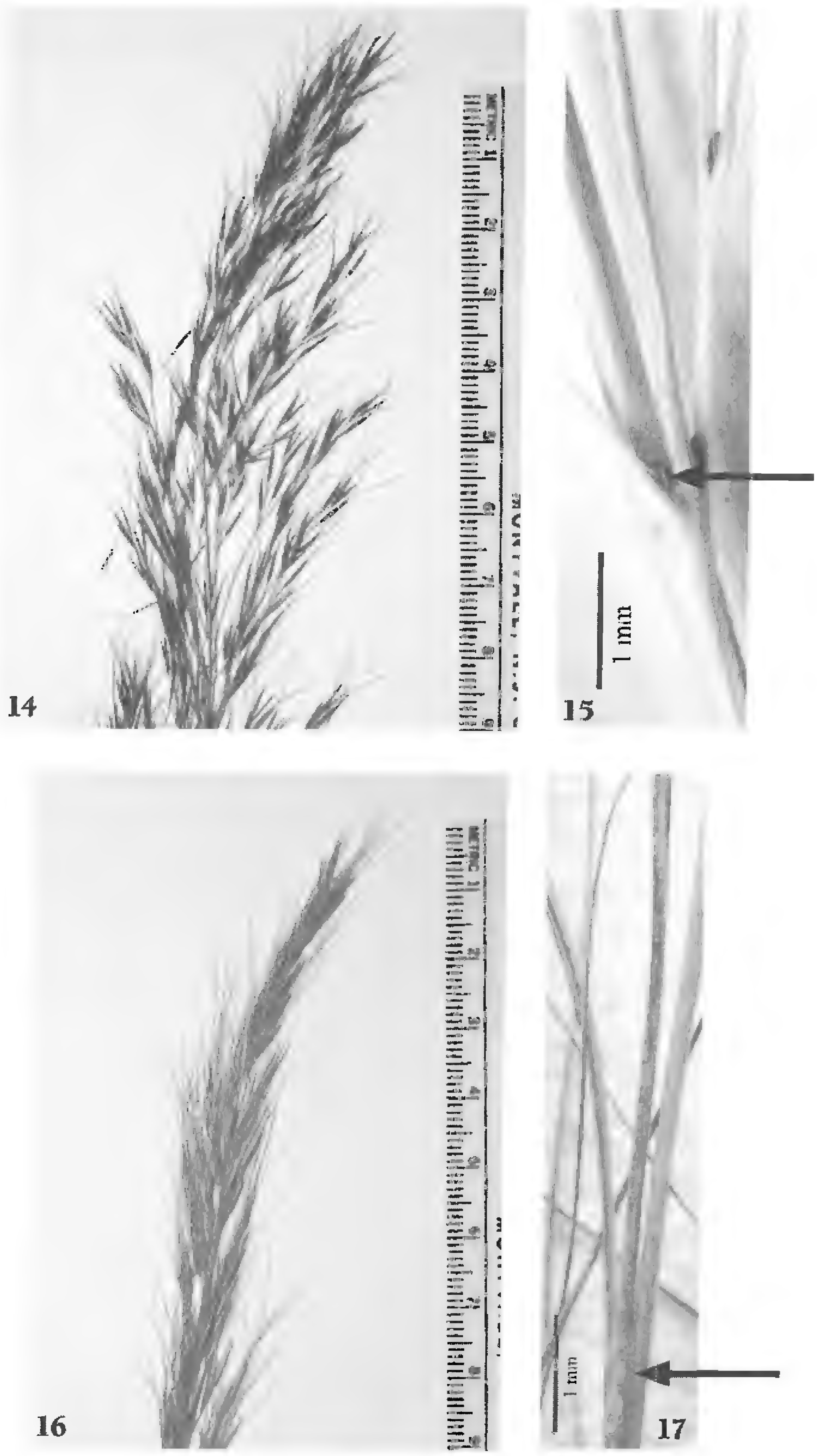


Fig. 13. Dispersion of OTUs along components I and II of PCA of specimens corresponding to the Group 2 cluster: S = type of *A. sorzogonensis*. O = isosyntype of *A. orizabensis* (*Müller 2103*, US). Black triangles = pulvinate form. Gray triangles = non-pulvinate form.

Table 4. Factor loadings for the first three components of the principle component analysis of Group 2 OTUs. Loadings less that ±0.250 have been replaced by zero.

	Component 1	Component 2	Component 3
Blade adaxial pubescence	0	0	0
Central awn length	0.451	0.309	0
Blade curling	0	0	0
Culms branching	0	0	0
Glume 1 length	0.468	0	-0.262
Glume 2 length	0.427	-0.376	0
Blade involution	0	0	0
Lateral awn length	0.466	0	0
Callus to awn length	0.407	0	0
Blade margins	0	0	0
Node shape	0	0	0
Pulvini	0	0.516	-0.815
Panicle length	0	0.615	0.406
Total	48.1%	22.4%	11.5%



Figs. 14–17. 14. Open panicle with pulvini in the axils of the panicle branches and pedicels. **15.** Pulvini in axils of pulvinate panicle (arrow). **16.** Contracted panicle lacking pulvini in the axils of the panicle branches. **17.** Axils lacking pulvini (arrow).

within *A. purpurea* and *A. pansa* (Allred 1984a; Allred & Valdes-Renya 1997) forma are recognized based on pulvini development:

KEY TO THE FORMS OF *ARISTIDA SORZGONENSIS*

Panicles pulvinate, with pulvini in the axils of branches, branchlets and pedicels, the panicle at least slightly open and somewhat diffuse _____ **4a.** f. ***sorzogonensis***

Panicles non-pulvinate, rarely developing pulvini in the axils of branches, branchlets or pedicels, the panicle consistently narrow and contracted _____ **4b.** f. ***orizabensis***

Table 5. Comparison of features of *Aristida gibbosa, A. sorzogonensis,* and *A. marginalis.*

	A. gibbosa		**A. sorzogonensis**				**A. marginalis**
		non-pulvinate			**pulvinate**		**type specimen**
Continuous Characters	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range	Range
Panicle length (cm)	17.6 ± 5.4	9.0–31	16.0 ± 4.9	6.5–25.0	19.7 ± 3.9	9.0–27.5	16.0–18.0
Glume 1 length (mm)	6.9 ± 1.1	4.9–10.3	9.0 ± 1.4	6.2–11.0	8.4 ± 1.6	4.8–10.7	7.2–8.0
Glume 2 length (mm)	6.2 ± 1.0	5.0–9.1	8.1 ± 1.3	6.0–10.5	7.4 ± 1.3	4.5–9.1	6.6–7.3
Callus to awn length (mm)	6.4 ± 1.4	4.8–11.0	9.7 ± 1.5	5.7–12.0	9.5 ± 1.7	5.7–13.0	6.2–7.3
Central awn length (mm)	11.1 ± 2.0	8.3–18.0	12.7 ± 2.4	8.4–17.5	12.8 ± 2.3	8.3–18.1	13.3–15.4
Lateral awn length (mm)	8.4 ± 1.7	6.0–14.0	10.2 ± 1.7	6.0–14.0	10.2 ± 2.5	5.5–15.8	9.5–12.1
Discrete Characters							
Culms	branched	unbranched	unbranched	branched			
Nodes	gibbous	terete	terete	gibbous			
Blades	stiff & erect	lax & curling	lax & curling	lax & curling			
involution	folded	flat	flat	flat			
margins	not thickened	thickened	thickened	thickened			
adaxial pubescence	glabrous	prominently pilose	prominently pilose	pilose			
Panicle	non-pulvinate	non-pulvinate	pulvinate	weakly pulvinate			

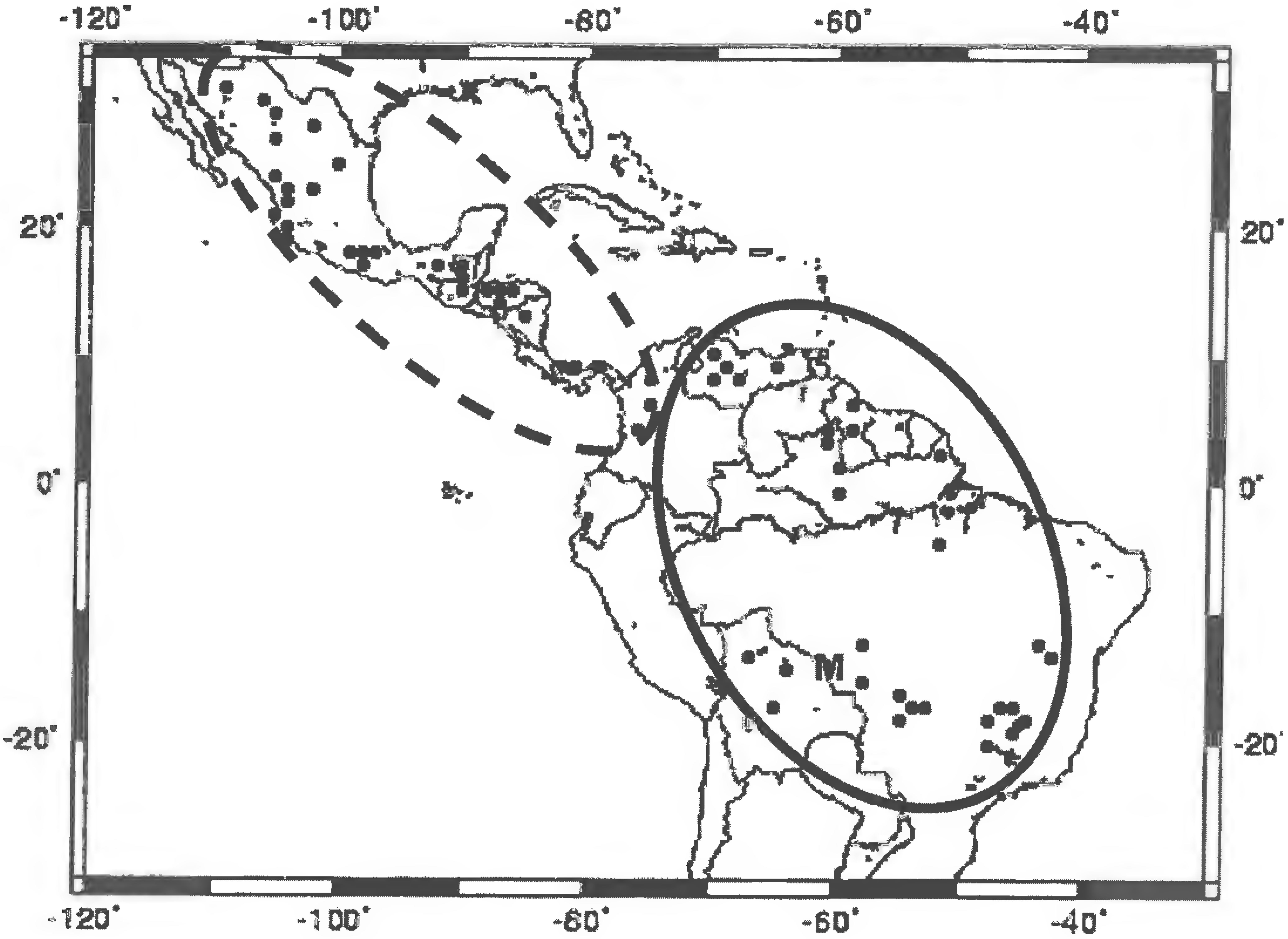


Fig. 18. Distribution map of species in the *Aristida gibbosa* complex. Circles indicate collection locations of herbarium specimens used in the study. Some dots represent more than one collection. Dashed line = *A. sorzogonensis*. Solid line = *A. gibbosa*, M = Type specimen of *A. marginalis*.

4a. Aristida sorzogonensis f. sorzogonensis

Distribution.—Mostly Mexico (Chiapas, Chihuahua, Jalisco, Michoacan, Nayarit, Sinaloa, Tepic) and Central America (Costa Rica, Honduras, Panama), with a few specimens from Columbia and Bolivia.

Specimens examined. **COLOMBIA. Santa Marta:** no locality, *H.H. Smith 136* (US). **BOLIVIA:** between Aguas Zembrades and Pinal,trail to Cerro SanLucas Bolivar, 1400 ft, 12 Aug 1944, *Drew, W.B. 146* (US). **COSTA RICA. Puntarenas:** 3 km N of the Carretera Interamericana along the road to Boruca, 12 Dec 1968, *Pohl et al. 11602* (F). **HONDURAS. El Paraiso:** Wuebrada del Muro, road to Yuscaran, open ground, 5 Nov 1951, *J.R. Swallen 11327* (MO). **Morazan:** Sabanas abiertas a lo largo de la carretena, Las Mesas, 23 Nov 1948, *A. Molina 1707* (US); rocky pine woods, hills around Zamorano valley, 2 Nov 1951, *Swallen J.R. 11259* (US); rocky pine-oak slopes, 15 Oct 1951, *J.R. Swallen 10751* (US); rocky pine woods, hills around Zamorano valley, 2 Nov 1951, *J.R. Swallen 11256* (US); colinas y bosque micto entre Las Mesas y Guayabillas 5km empalme carretera dalini yuscaran, 04 Nov 1963, *A. Molina 13164* (F). **MEXICO. Chiapas:** Municipio Chicocucelo, Belen, 1 km E of Las Sabanas, 2 km SE of Chicomucelo, 18 Nov 1984, *Davidse et al. 30037* (MO). **Chihuahua:** Rio Mayo; Upper sonoran; oak flat, Guasaremos, 26 Sep 1935, *H.S. Gentry 1873* (ARIZ, MO, NMCR, WIS, US). **Jalisco:** 20 km Guadalajara-Tepic, 26 Sep 1946, *Hernandez et al. 2745* (US); arroyo sin nombre (pero con agua corriente) 3.2 km al W de Las Marias; 15 km por camino al E de Cuautitlan en el camino a Avotitlan, 08 Jan 1985, *T.S. Cochrane 10987* (WIS). **Michoacan:** along road from Tsitzio-Tiquicheo-Huetamo-Altamirano, 7 Oct 1953, *E.R. Sohns 906* (US). **Nayarit:** 10 km al E de Tepic por la carretera a Mazatlan, 18 Nov 1983, *F.J. Santana 1426* (MO); 13 km NW of TEPIC (Municipio de Tepic) along highway 15, 18 Nov 1983, *Solheim et al. 971* (WIS); steep treeless hills 10 mi SE of Tepic, 6 Oct 1952, *Mcvaugh R 13384* (US). Sinaloa: Cerro Colorado, 1 Nov 1904, *Brandequa* (US); Mesa Malqueson, Cerro Colorado; open rocky slopes on oak savannah, 2500 ft, 8 Dec 1939, *H.S. Gentry 5179* (MO). **Sonora:** Sierra Tecurahui, SE Sonora, 4250 m, 27 Oct 1961, *Gentry et al. 19380* (US). **Tepic:** no locality, 6 Feb 1892, *Dr. E. Palmer 1916* (US). **PANAMA:** between Paso Del Arado and Ola, province of Cocle, in savannas and thickets, 7 Dec 1911, *H. Pittier 5019* (US); vicinity of Ola, province of Cocle, 7 Dec 1911, *H. Pittier 5047* (US); Picacho de Ola, province of Cocle, 8 Dec 1911, *H. Pittier 5066* (US); ca. 10 km SW of San Carlos along the Inter-American Hwy, 18 Nov 1975, *Davidse et al. 10128* (MO).

4b. Aristida sorzogonensis f. **orizabensis** (E. Fourn.) Strahan & Allred, comb. nov. Basionymn: *Aristida orizabensis* E. Fourn., Mexicanas Plantas II:78. 1886. Type: MEXICO. Veracruz: Valle de Orizaba, *J.H. Schaffner 136* (syntypes: P; isosyntypes LE); MEXICO: *F. Müller 2103* (syntype: P; isosyntypes: L, NY! US!). The name *Aristida orizabensis* E. Fourn. remains to be lectotypified, being based on two collections (*Schaffner 136* and *Müller 2103*) cited by Fournier (1886). The specimens at P and LE were unavailable. Our concept of *Aristida orizabensis* Fournier is based on isosyntypes of *Müller 2103* at NY and US.

Distribution.—Mostly Central America (Guatemala, Honduras, Panama), with fewer specimens from Mexico (Sinaloa, Guerrero) and Columbia.

Specimens examined. **COLOMBIA. Huila:** 3 km SE of Neiva, Huila, 1700 m, 23 Feb 1945, *Little et al. 9470* (US); 6 km SE of Altamira along road to Florencia, 9 Jan 1974, *G. Davidse 5602* (MO). **GUATEMALA. Jalapa:** dry rocky pine-clad between Monjos and Jalapa, ca. 10 mi S Jalapas, 29 Nov 1939, *J. Steyermark 32176* (F). **Without State:** in wet ground in margin of oat field between Guatemal city and Jutiapa, 10 Oct 1944, *Goodman et al. 3696* (F). **HONDURAS. El paraiso:** road to Yuscaran open places, about km 2, 5 Nov 1951, *J.R Swallen 11351* (US); rocky slope, in pine woods, beyond Rio San Francisco, 1 Nov 1951, *J.R. Swallen 11212* (US). **Morazan:** 20 km N of Talanga along the road to Cedros Pinus-Quercus forest on hills, 4 Oct 1986, *Davidse et al. 31584* (MO); Santa Ines, 4 Nov 1943, *J.V. Rodriguez 1486* (F); open grassy hills, 7 Nov 1951, *J.R. Swallen 11386* (US); Santa Inez, 5 km E of El Zamarano, 19 Dec 1978, *Pohl et al. 13738* (MO); Colinas y bosque mixto entre Las Mesas y Guayabillas, 5 km empalme carretera dalini yuscaran, 04 Nov 1963, *A.Molina 13167* (F). **Without State:** in mixed oak-pine forest near Piedra Herrada, 11 Sep 1949, *L.O. Williams 15975* (F); in pine woods, near Jicarito, 5 Dec 1948, *Williamson et al. 14802* (US). **MEXICO. Guerrero:** Ixtapan de la Sal, 12 Oct 1952, *Matuda et al. 27056* (US). **Sinaloa:** between Mazatlan and Durango, 6 Jan 1975, *Beetle et al. 3695* (WIS). **PANAMA. Herrera:** 10 mi S Ocu roadside, 21 Jan 1966, *Tyson et al. 2866* (MO).

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TAXONOMY OF *BROMUS* (POACEAE: POOIDEAE: BROMEAE) SECTIONS *BROMOPSIS*, *BROMUS*, AND *GENEA* IN BRITISH COLUMBIA, CANADA

Jeffery M. Saarela

Canadian Museum of Nature
P.O. Box 3443, Station D
Ottawa, ON K1P 6P4, CANADA
jsaarela@mus-nature.ca

ABSTRACT

A taxonomic treatment of *Bromus* sections *Bromopsis*, *Bromus* and *Genea* in British Columbia, Canada, is presented. Nineteen taxa are recognized, including six native and 12 introduced species, one with two varieties. The introduced species *B. riparius*, promoted in western North America for forage, is reported from British Columbia for the first time, with discussion of its North American introduction history and morphology. *Bromus squarrosus* var. *villosus* is reported from British Columbia, representing the first report of this taxon for the province and for North America. *Bromus kalmii* var. *occidentalis* Vasey ex Beal is lectotypified. Keys for determining the species, synonymies, descriptions, distribution maps, representative specimens and illustrations are provided for each of the species.

RESUMEN

Se presenta un tratamiento taxonómico de *Bromus* secciones *Bromopsis*, *Bromus* y *Genea* en British Columbia, Canadá. Se reconocen diez y nueve taxa, que incluyen seis especies nativas y 12 introducidas, una con dos variedades. La especie introducida *B. riparius*, fomentada en el oeste de Norte América para forraje, se cita de British Columbia por primera vez, con discusión sobre su morfología e historia de su introducción en Norte América. Y se cita *Bromus squarrosus* var. *villosus* de British Columbia, siendo la primera cita de este taxon para la provincia y para Norte América. Se lectotipifica *Bromus kalmii* var. *occidentalis* Vasey ex Beal. Se aportan claves para identificar las especies, sinonimias, descripciones, mapas de distribución, especimenes representativos e ilustraciones de todas las especies.

Bromus L. is a large and taxonomically complex grass genus that includes more than 160 species distributed in temperate regions worldwide. The genus is distinguished from other grass genera by the combination of leaf sheaths that are closed for most of their length, awns that are inserted subapically and hairy appendages on the apices of the ovary (Clayton & Renvoize 1986). Approximately 80 *Bromus* species are currently recognized in North, Central and South America (Pavlick et al. 2003); 29 of these reportedly occur in Canada (Pavlick & Anderton 2007). Among the 10 Canadian provinces and three territories (Fig. 1), the westernmost and topographically diverse British Columbia has the greatest number of *Bromus* species. *Bromus* is the second-largest grass genus in British Columbia; only *Poa* L., with 31 species (Soreng 2007), has greater species richness in the province.

In North America most workers recognize five sections in *Bromus* (reviewed by Saarela et al. 2007), but multiple recent molecular phylogenetic studies indicate that not all are natural groups, particularly the globally widespread *B.* sect. *Bromopsis* Dumort., which appears to comprise distinct Sierra Madrean (Mexican), North American, South American and Eurasian lineages (e.g., Pillay & Hilu 1990, 1995; Saarela et al. 2007). More work is needed to clarify higher-level phylogenetic relationships in *Bromus*. Nonetheless, the traditionally recognized *Bromus* sections can generally be recognized morphologically and learning their key characteristics can greatly aid in species identification in the field and herbarium.

There has been considerable progress in clarifying lower-level taxonomic problems in *Bromus*. Several species that occur in North American have received recent taxonomic study, including: *B. ciliatus* L. and *B. richardsonii* Link (Peterson et al. 2002); *B. grandis* (Shear) Hitchc., *B. hallii* (Hitchc.) Saarela & P.M. Peterson and *B. orcuttianus* Vasey (Saarela et al. 2005); *Bromus catharticus* var. *elata* (E. Desv.) Planchuelo (Planchuelo 2006); and *B. carinatus* Hook. & Arn. (Barkworth et al. 2006). Similar recent taxonomic work has been conducted on taxa from South America (Massa et al. 2001, 2004; Saarela et al. 2006) and Eurasia (Sales 1993, 1994; Spalton 2002). Comprehensive taxonomic treatments of *Bromus* for North America north of Mexico

Fig. 1. Map of Canada, with the 10 provinces and three territories indicated. British Columbia is the western-most Canadian province. Scale bar = 500 km.

have also recently been published (Pavlick 1995; Pavlick & Anderton 2007), but despite these resources, identifying species of *Bromus* can be notoriously difficult for many workers. In such large and difficult groups, geographically focused taxonomic treatments can greatly facilitate accurate identifications and provide more detailed information than is normally found in standard floras, be they regional or continental in scope. The most recent comprehensive treatment of *Bromus* for British Columbia, in *Illustrated Flora of British Columbia* (Douglas et al. 2001), takes a taxonomically conservative approach and no longer reflects current understanding of the genus. Another recent treatment (Stewart & Hebda 2000) is restricted geographically to only those species that occur in the Columbia Basin region of British Columbia. The purpose of this work is to provide a detailed and updated taxonomic treatment for *Bromus* in British Columbia, including a dichotomous key, synonymies, species descriptions, distribution maps and citations of representative specimens.

Bromus in British Columbia

Bromus in British Columbia includes multiple native and introduced species that are currently classified in four sections. Most of the introduced species are annuals classified in *B.* sects. *Bromus* (*B. briziformis* Fisch. & C.A. Mey., *B. commutatus* L., *B. hordeaceus* L., *B. japonicus* Thunb., *B. racemosus* L., *B. secalinus* L. and *B. squarrosus* L.) and *Genea* Dumort. (*B. diandrus* Roth, *B. sterilis* L. and *B. tectorum* L.). All of these (and other) introduced species in *B.* sects. *Bromus* and *Genea* occur throughout western North America, mostly north of Mexico (see Pavlick & Anderton 2007; Saarela & Peterson in press), and several have caused serious ecological disruption. In general, annual species can be distinguished from perennial species based on basal vegetative characteristics. In perennial *Bromus* species, the dried remains of the previous years' growth are normally present, whereas there is no previous years' growth in the annual species. In most cases the annual taxa are generally smaller in stature and have a more delicate appearance (with some exceptions, such as some individuals of the large annual, *B. diandrus*), compared to the perennial taxa. *Bromus* sect. *Bromus* is characterized by 3–5-nerved first glumes, 5–7-nerved second glumes and lemmas rounded over the backs,

whereas *B.* sect. *Genea* is characterized by 1(–3)-nerved first glumes, 3(–5)-nerved second glumes and narrow, elongate lemmas. Species of *B.* sect. *Bromopsis* in British Columbia are perennials with 1(–3)-nerved first glumes, 3(–5)-nerved second glumes and lemmas rounded or slightly keeled over the backs (i.e., flattened dorsiventrally). Two *B.* sect. *Bromopsis* species in British Columbia are introduced: the highly invasive smooth brome (*B. inermis* Leyss.) and meadow brome (*B. riparius* Rehm.), which is reported here as part of the British Columbia flora for the first time. The remaining five *B.* sect. *Bromopsis* species in the province are native: *B. ciliatus* L., *B. pacificus* Shear, *B. pumpellianus* Scribn., *B. richardsonii* Link and *B. vulgaris* (Hook.) Shear. The remainder of the *Bromus* taxa in British Columbia are classified in *B.* sect. *Ceratochloa* (P. Beauv.) Griseb., a group that is widespread throughout the province and easily recognizable on the basis of its strongly laterally flattened and keeled glumes and lemmas. Species limits within *B.* sect. *Ceratochloa* are not clear, both in British Columbia and more broadly throughout western North America. Taxa in *B.* sect. *Ceratochloa* have been variously recognized at different ranks; in British Columbia these include *B. aleutensis* Trin. ex Griseb. [=*B. sitchensis* Bongard var. *aleutensis* (Trin. ex Griseb.) Hultén], *B. carinatus* Hook. & Arn., *B. marginatus* Steud. [=*B. carinatus* var. *marginatus* (Nees.) Barkworth & Anderton], *B. polyanthus* Scribn. ex Shear and *B. sitchensis* Bongard (e.g., Calder & Taylor 1968; Hitchcock et al. 1969; Hubbard 1969; Pavlick 1995; Douglas et al. 2001; Clayton et al. 2002 onwards; Barkworth et al. 2006; Pavlick & Anderton 2007). Because taxon circumscriptions are not clear in *B.* section *Ceratochloa*, the section is not treated here (although it is included in the key).

MATERIALS AND METHODS

This study is based on study of over 1200 herbarium specimens from CAN, DAO, UBC, US and V, and observations made in the field from 2003–2007. The morphological descriptions are new and are based mostly on study of herbarium specimens collected in British Columbia. For a subset of introduced species for which there are not a lot of collections, Eurasian specimens at CAN were also used to generate the descriptions. Nomenclatural information was compiled through study of the primary literature and numerous secondary sources, including Pavlick (1995) and Pavlick et al. (2003). I have not attempted to account for all of the names that have been applied to the introduced taxa in their native European ranges (i.e., species of *B.* sects. *Bromus* and *Genea*); these names are rarely used in the North American literature. Information on common names (in English and French) was obtained through internet searches and from information presented by Darbyshire (2003). Data on geographical distribution, elevation and habitat are based on herbarium specimen label data and personal field observations. Where not available on specimen labels, geographical information was obtained from the Geographical Names of Canada website (http://geonames.nrcan.gc.ca/index_e.php, accessed 2007). Maps were produced in ArcView (Environmental Systems Research). All illustrations were prepared by Dr. Cynthia T. Roché, published originally in Flora of North America volume 24 (Barkworth et al. 2007); they are used here with permission.

TAXONOMIC TREATMENT

Bromus L., Sp. Pl. 1:76. 1753. Type: *Bromus secalinus* L. (conserved type: LINN 93.1, see Jarvis, Taxon 41:559. 1992, and Taxon 44:611–612. 1995).

Plants annual or perennial; usually caespitose, occasionally rhizomatous. Culms 7–172 cm tall, one to several per plant. Leaf sheaths closed for most of their length, glabrous or variously pubescent; auricles present or absent; ligules membranous, to 7 mm long; blades flat, abaxial and adaxial surfaces glabrous or variously pubescent. Inflorescences panicles, sometimes racemose, occasionally reduced to a single spikelet, open to dense, erect to nodding. Spikelets 1.3–8 cm long, terete or compressed dorsiventrally to laterally, disarticulation above the glumes and below the lemmas. Glumes unequal, shorter than the adjacent lemma, glabrous or variously pubescent, acute, sometimes mucronate; lower glumes 1–7(9)-veined; upper glumes 3–9(11)-veined. Lemmas rounded to keeled, glabrous or variously pubescent, with a single ±terminal or subterminal awn, occasionally unawned; paleas shorter than lemmas, usually variously ciliate on the keels. Styles 2, inserted laterally on a bilabiate appendage of the ovary. Anthers 2–3. Base chromosome number, $x = 7$.

Etymology.—The name *Bromus* is derived from the Greek *bromos*, which means 'oats'; *bromos* is derived from *broma*, an ancient Greek word for food (Wagnon 1952; Pavlick & Anderton 2007).

KEY TO THE SPECIES OF *BROMUS* SECTIONS *BROMUS*, *BROMOPSIS* AND *GENEA* IN BRITISH COLUMBIA

1. Spikelets laterally compressed; lemmas laterally compressed and strongly keeled (B. sect. Ceratochloa, not treated here).
1. Spikelets not laterally compressed; lemmas flattened dorsiventrally, not strongly keeled.
  2. Lemmas narrow, largest lemmas generally < 2 mm wide; lemma apex bidentate, with awn-like to acuminate hyaline teeth 1–5 mm long (B. sect. Genea).
    3. Lemma bodies 18–35 mm long; awns 30–50 mm long; lower glumes 12–26 mm long; upper glumes 18–35 mm long ____ **4. B. diandrus**
    3. Lemma bodies 9–22 mm long; awns < 30 mm long; lower glumes 4–14 mm long; upper glumes 7–21 mm long.
      4. Lemmas 13–22 mm long; awns 15–30 mm long; panicles sparse, with 1(–3) spikelets per branch; branches straight, usually longer than spikelets ____ **16. B. sterilis**
      4. Lemmas 9–13.8 mm long; awns 8–18 mm long; panicles sparse or dense, usually some branches with > 3 spikelets per branch; branches sinuous, longer or shorter than spikelets ____ **17. B. tectorum**
  2. Lemmas broad, largest lemmas generally > 2 mm wide (except in B. vulgaris) and conspicuously flattened across the back; lemma apex entire or bidentate, teeth usually not hyaline, 0–3 mm long, not awn-like or acuminate.
    5. Plants perennial, often with remnants of a previous years' vegetative growth present; lower glumes 1–3-nerved; upper glumes 3–5-nerved (B. sect. Bromopsis).
      6. Plants with rhizomes; longest anthers > 4 mm long.
        7. Awns (3–)4–7.1 mm long; readily decaying basal sheaths reticulate-fibrillose (i.e., thatched in appearance); cilia present on palea keels only along upper 2/3 to upper half; marginal leaf blade hairs robust and conspicuously widened at the base ____ **13. Bromus riparius**
        7. Awns 0–4 mm long; basal sheaths eventually decaying into straight fibers; cilia present on palea keels along lower ¾ to entire length; leaf blades glabrous or pubescent, marginal hairs (if present) not robust and not conspicuously widened at the base.
          8. Awns absent or up to 3 mm long; lemmas glabrous to variously scabrous or puberulent on lower 1/6 to 1/4 ____ **6. B. inermis**
          8. Awns 1–4.5(–5) mm long; lemmas with hairs 0.5–0.8 mm long along margins and midvein, or moderately to densely villous throughout ____ **10. B. pumpellianus**
      6. Plants without rhizomes, all anthers < 4 mm long.
        9. Most lower glumes 3-nerved; awns 1.5–3(–4) mm long ____ **9. B. porteri**
        9. Most lower glumes 1-nerved; awns (2–)3–11 mm long.
          10. Glumes pubescent.
            11. Mature inflorescences open, 13–19 cm wide; branches broadly spreading, each with (1–)2–5 spikelets; awns 3–6.5(–7) mm long; ligules 2–4 mm long; leaf blades not thin and papery in herbarium material ____ **8. B. pacificus**
            11. Mature inflorescences narrow, 1–5 cm wide; branches erect, narrowly ascending or drooping, each with 1(–2) spikelets; awns (4–)6–11 mm long; ligules(2–)3–6(–7) mm long; leaf blades thin and papery in herbarium material ____ **18. B. vulgaris**
          10. Glumes glabrous.
            12. Ligules (2–)3–6(–7) mm long; awns (4–)6–11 mm long; larger lemmas ≤ 2 mm wide; leaf blades thin and papery in herbarium material ____ **18. B. vulgaris**
            12. Ligules 0.5–3 mm long; awns 4–7(–9) mm long; larger lemmas generally > 2 mm wide; leaf blades not thin and papery in herbarium material.
              13. Lemma backs glabrous or sparsely puberulent with hairs to 0.1 mm long, margins pubescent with hairs 0.5–1.3 mm long; upper glumes 6.5–9.5 mm long; lower glumes 5–7.5 mm long; anthers 0.9–1.6 mm long; basal leaf sheaths glabrous or sparsely to densely pubescent with soft and wavy hairs; upper blades with pilose adaxial surfaces; upper nodes usually pubescent ____ **2. B. ciliatus**
              13. Lemma backs sparsely to densely pubescent with hairs > 0.1 mm long; upper glumes (8–)9.5–11.5(–14.5) mm long; lower glumes 7–9.5 mm long; anthers (1.2–)1.6–2.7(–3.4) mm long; basal leaf sheaths glabrous or sparsely to densely pubescent with stiff hairs; upper blades with glabrous adaxial surfaces; upper nodes usually glabrous ____ **12. B. richardsonii**

5. Plants annual, without remnants of a previous years' vegetative growth present; lower glumes 3–5-nerved; upper glumes 5–9-nerved (B. sect. Bromus).
   14. Lemmas appearing inflated, 3–4 mm wide; awns absent or to 1 mm long; spikelets ovate ____ **1. B. briziformis**
   14. Lemmas not appearing inflated, < 3 mm wide; awns 2–20 mm long; spikelets lanceolate to ovate-lanceolate.
      15. Lemmas with strongly protruding nerves when dry; panicles usually dense ____ **5. B. hordeaceus**
      15. Lemmas smooth, without strongly protruding nerves; panicles ± open.
         16. Awns arising 1.5–5 mm below the apex of the lemma.
            17. Inflorescense usually racemose and appearing one-sided, the branches usually bearing a single spikelet; lemmas with hyaline margins 0.5–0.9 mm wide ____ **15. B. squarrosus**
            17. Inflorescences usually paniculate and not appearing one-sided, at least the lower branches usually bearing > 1 spikelet; lemmas with hyaline margins 0.3–0.5 mm wide ____ **7. B. japonicus**
         16. Awns arising < 1.5 mm below the apex of the lemmas.
            18. Lower leaf sheaths glabrous or with sparse, stiff hairs 0.5–0.6 mm long; spikelets widening substantially by divergence of the florets as the fruit forms, many rachillas becoming visible as the lemma wraps around the caryopses; caryopses U- and V-shaped in cross section ____ **14. B. secalinus**
            18. Lower leaf sheaths densely pubescent with long, soft hairs to 1.2 mm long; spikelets not widening substantially as the fruit forms, lemmas continuing to obscure most rachillas; caryopses flat or crescent shaped in cross section.
               19. Panicles narrow, < 2.5 cm wide; inflorescence branches < 4 cm (as measured from node to apex of the terminal floret); 1 spikelet per branch; most larger spikelets < 22 mm long (including awns); lemmas 6.5–9.5 mm long ____ **11. B. racemosus**
               19. Panicles broad and spreading, > 2.5 cm wide; longest inflorescence branches > 4 cm (as measured from node to apex of the terminal floret); 1–3 spikelets per branch; larger spikelets > 22 mm long (including awns); lemmas 7.5–11 mm long ____ **3. B. commutatus**

1. Bromus briziformis Fisch. & C.A. Mey., Index Sem. (St. Petersburg) 3:30. 1837. (**Figs. 2A–E, 3A**). TYPE: IRAN: Tahlysh, in locis aridis montosis prope pag. Limar, 1830, *C. Meyer s.n.* (HOLOTYPE: LE).

Annual; rhizomes absent; plants 17–70 cm tall. Culms 1–2 mm wide at base, smooth; nodes 2, brown-black, pubescent, hairs to 0.2 mm long. Leaf sheaths closed for most of their length, densely pilose with soft hairs to 0.6 mm; auricles absent; ligules 0.5–2 mm long, membranous, glabrous, erose; blades 5.5–10.2 cm long, 1.5–5 mm wide, abaxial surface densely pubescent with short, stiff hairs 0.1–0.3 mm long or densely pilose with long, soft hairs to 1.2 mm long, adaxial surface densely pilose with long, soft hairs to 1.2 mm long, margins smooth or serrulate. Panicles 5–11.5 cm long, 2–6 mm wide, open, lax and somewhat sparse, racemose, often appearing one-sided (secund); branches usually longer than spikelets, scabrous, 1(–2) spikelets per branch, lowest inflorescence node with 1–3 branches. Spikelets 1.8–2.5 cm long, ovate, rachillas not visible at maturity, florets 7–18. Glumes subequal, glabrous; lower glumes 4.6–6 mm long, 3–5-nerved; upper glumes 5–8 mm long, 5–9-nerved. Lemmas 6–9 mm long, 3–4.5 mm wide, 7–9-nerved, nerves not conspicuous, strongly angled near middle, glabrous or puberulent, hyaline margins 0.5–1.1 mm wide at widest point, apex minutely bifid, the cleft 0.1–0.3 mm deep; awn absent or to 1 mm long. Paleas 6.1–6.6 mm long, glabrous. Stamens 3; anthers 0.7–1 mm long, dark brown. $2n = 14$.

Distribution and Habitat.—Introduced. *Bromus briziformis* is native to Eurasia. In British Columbia it is known only from a handful of populations near the Canada/ U.S.A. border (Fig. 3A). It has been collected in the northwestern United States and in a few scattered locations in central and eastern North America (Pavlick & Anderton 2007). Habitats include waste places, roadsides and other disturbed areas. Elevation: 600–914 m.

Common Names.—rattlesnake brome, rattlesnake bromegrass, rattlesnake chess, rattlegrass.

Notes.—*Bromus briziformis* is an annual species that superficially resembles the quaking grasses (*Briza* L.; the introduced *B. major* and *B. minor* are reported from British Columbia), but it is easily distinguished

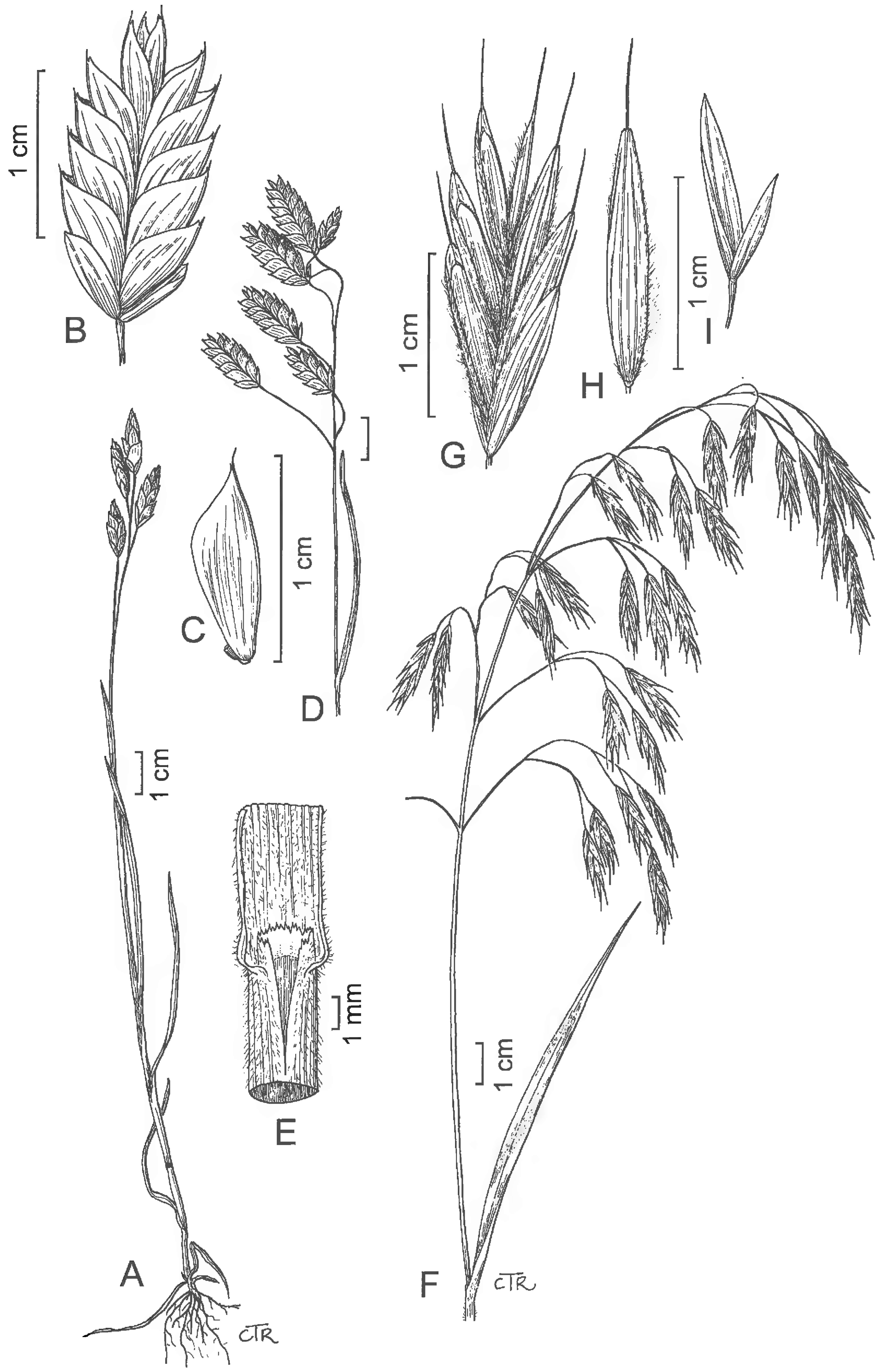

Fig. 2. ***Bromus briziformis.*** **A. Habit. B. Spikelet. C. Lemma. D. Inflorescence. E. Ligule.** ***Bromus ciliatus.*** **F. Inflorescence. G. Spikelet. H. Lemma. I. Glumes.**

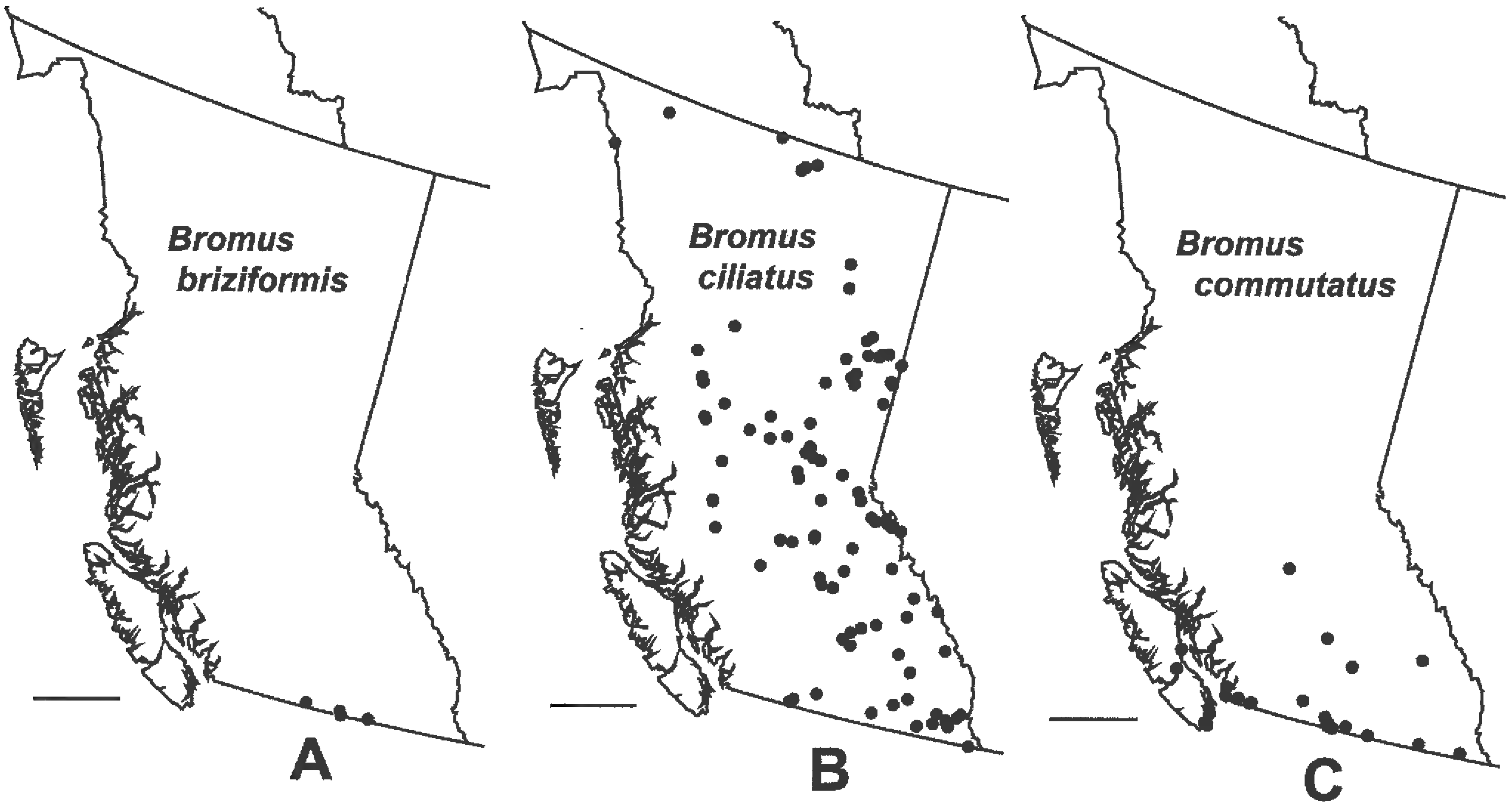

Fig. 3. Geographic distribution in British Columbia. A. *Bromus briziformis*. B. *Bromus ciliatus*. C. *Bromus commutatus*. Scale bars = 200 km.

from species of *Briza* by its closed leaf sheath. It is easily distinguished from all other *Bromus* species on the basis of its wide lemmas.

Representative Specimens Examined. **CANADA. British Columbia:** near International Boundary between Kettle and Columbia rivers, 10 Jun 1902, *J.M. Macoun 63326* (US); Spotted Lake, ca. 2.5 km W of Osoyoos Lake, 12 Jun 1991, *Douglas 12535* (UBC, V); 2.3 km E of Granby River, 500 m N of Sandy Creek Forest Service Road, about 5 km due N of Grand Forks, 2700 ft, 15 Jun 1996, *F. Lomer 96-60* (UBC, V); 400 meters E of Charbonneau Creek, 200 m N of Pend d'Oreille Road, about 3.5 km E of 7 Mile Dam, 20 km SE of Trail, 12 Jun 1996, *F. Lomer 96-44* (UBC).

2. Bromus ciliatus L., Sp. Pl. 1:76–77. 1753. (**Figs. 2F–I, 3B**). *Bromus inermis* var. *ciliata* (L.) Trautv., Acta Horti Petrop. 5:135. 1877. *Bromus purgans* var. *ciliatus* (L.) Kuntze, Revis. Gen. Pl. 2:763. 1891. *Forasaccus ciliatus* (L.) Lunell, Amer. Midl. Naturalist 4:225. 1915. *Bromus ciliatus* var. *genuinus* Fernald, Rhodora 32:70. 1930. *Zerna ciliata* (L.) Henrard, Blumea 4:498. 1941. *Bromopsis ciliata* (L.) Holub, Folia Geobot. Phytotax. 8:167. 1973. Type: U.S.A. New York: Essex Co., Huntington Wildlife Forest Station, Newcomb, sand pit E of Ranger Station, 1600 ft, 23 Jul 1939, *H.F. Heady 768* (neotype: DAO-53967, designated by McNeill, Taxon 25:613. 1976; isoneotype: US).

Bromus canadensis Michx., Fl. Bor.-Amer. 1:65. 1803. *Bromus hookeri* var. *canadensis* (Michx.) E. Fourn., Mexic. Pl. 2:128. 1886. *Zerna canadensis* (Michx.) Tzvelev, Novosti Sist. Vyss. Rast. 7:54. 1970 [1971]. *Bromopsis canadensis* (Michx.) Holub, Folia Geobot. Phytotax. 8:167. 1973. Type: CANADA: Lac St. Jean, *Michaux s.n.* (holotype: P; isotype: US-A0865520, fragment ex P, photostat!).

Bromus purgans var. *pallidus* Hook., Fl-Bor. Amer. 2:252. 1840. *Bromus richardsonii* var. *pallidus* (Hook.) Shear, Bull. Div. Agrostol., U.S.D.A. 23:34. 1900. Type: CANADA: Saskatchewan to the Rocky Mountains, *Drummond s.n.* (holotype: K; isotype: US-A865461, fragment).

Bromus ciliatus f. *denudatus* Wiegand, Rhodora 24:91. 1922. *Bromus ciliatus* var. *denudatus* (Wiegand) Fernald, Rhodora 28:20. 1926. *Bromus ciliatis* subv. *denudatus* (Wiegand) Farw., Amer. Midl. Naturalist 10:203. 1927. Type: U.S.A. Massachusetts: Ashfield, 3 Aug 1909, *E.F. Williams s.n.* (holotype: GH; isotype: US-865527!, fragment).

Bromus ciliatus var. *intonsus* Fernald, Rhodora 32:70. 1930. *Bromus ciliatus* f. *intonsus* (Fernald) F. Seym., Fl. N. England 60. 1969. Type: U.S.A. Massachusetts: Ashfield, 4 Aug 1909, *E.F. Williams s.n.* (holotype: GH; isotype: US-865526!, fragment ex GH).

Bromus dudleyi Fernald, Rhodora 32:63, pl. 196. 1930. Type: CANADA. Newfoundland: bushy swale along Deer Brook, Bonne Bay, 26 Aug 1929, *M.L. Fernald, Long & Fogg 1223* (holotype: GH; isotype: US-865487!, fragment ex GH).

Perennial; rhizomes absent; plants 55–149 cm tall. Culms 1.2–4 mm wide at base, smooth; nodes 4–6, brown, pubescent, hairs 0.2–0.5 mm long. Leaf sheaths closed for most of their length, glabrous or sparsely to densely pubescent with soft, wavy hairs to 1.6 mm long; auricles absent; ligules 0.5–1.6 mm long, membranous, glabrous or minutely pubescent, erose; blades 10–27 cm long, 4–12 mm wide, adaxial surfaces pubescent with soft, wavy hairs 0.3–1.3 mm long, abaxial surfaces glabrous, margins smooth or

serrulate. Panicles 8–21 cm long, 3.5–10.5 cm wide, open; branches ascending to spreading or drooping, shorter or longer than spikelet, glabrous or scabrous, 1–4 spikelets per branch, lowest inflorescence node with 1–5 branches. Spikelets 2.2–3 cm long (including awns); florets 4–9. Glumes subequal, lanceolate, glabrous, keels ± scabrous; lower glumes 5–7.5 mm long, 1(–3)-nerved; upper glumes 6.5–9.5 mm long, 3(–5)-nerved, sometimes mucronate with mucros to 0.2 mm long. Lemmas 8–14 mm long, 1–2.5 mm wide, 7-nerved, pubescent along margins with hairs 0.5–1.3 mm long, hairs sometimes restriced to lower 1/3, backs glabrous or puberulent with hairs to 0.1 mm long, apex entire or minutely bifid, the cleft to 0.2 mm deep; awns (1–)2–6.5 mm long, arising 0–0.2 mm below lemma apex, straight, antrorsely scabrous. Paleas 7.4–9.2 mm long, shorter than lemmas, keels ciliate, cilia to 0.5 mm long. Stamens 3; anthers 1–1.7 mm long, dark brown. $2n = 14$.

Distribution and Habitat.—Native. *Bromus ciliatus* is the widest-ranging native *B.* sect *Bromopsis* species in North America. It occurs across the continent, absent only in south-central and south-eastern U.S.A. (Pavlick & Anderton 2007). *Bromus ciliatus* occurs throughout British Columbia, mostly east of the coastal mountain ranges (Fig. 3B). Its distribution is sympatric with that of *B. richardsonii*, but *B. ciliatus* generally occurs at lower elevations (Peterson et al. 2002). *Bromus ciliatus* occurs in a wide range of habitats, including wet ditches, roadsides, boggy areas, dry terraces, moist woodlands, forest openings, stream banks, rocky flats and grassy areas. Elevation: 396–1554 m.

Common Names.—English: fringed brome; French: brome cilié.

Notes.—*Bromus ciliatus* and *B. richardsonii* have been variously treated as the same or separate taxa (see comments under *B. richardsonii*). Peterson et al. (2002) demonstrated that these taxa are morphologically and genetically distinct and appropriately recognized at the species level. Because *B. ciliatus* occurs in a variety of habitats, there is interest, particularly in western Canada, for developing ecological cultivars for re-seeding disturbed areas and clearcuts (see May et al. 1998, 1999; Fu et al. 2005). Fu et al. (2005) used AFLP data to examine molecular variation within and among *B. ciliatus* populations across Canada and found high among-population variation and low within-population variation.

Representative Specimens Examined. **CANADA. British Columbia:** Yellowhead Pass, Rocky Mtns, 20 Jul 1848, *W.S. Spreadborough 21012* (US); Sand Creek, Kootenay Valley, 23 Jul 1883, *Dawson s.n.* (CAN); Six-mile Creek, Selkirk Mtns, 8 Aug 1885, *J. Macoun 72994* (US); Selkirk Mountains, Six-mile Creek, 8 Aug 1885, *J. Macoun 72997* (CAN); Sicamous, 3 Jul 1889, *J. Macoun 30013* (CAN); McLennnan River headwaters of Columbia River, 27 Jul 1898, *W.S. Spreadborough s.n.* (CAN); Armstrong, 27 Aug 1904, *E. Wilson 415* (UBC); Armstrong, 31 Aug 1904, *E. Wilson 421* (UBC); Salmon Arm, 15 Aug 1911, *M.O. Malte s.n.* (CAN); Salmon Arm, 15 Aug 1911, *M.O. Malte s.n.* (DAO); McBride, 2360 ft, Jun-Jul 1914, *J.A. Walker s.n.* (UBC); Hazelton, 17 Jul 1917, *J.M. Macoun 93974* (CAN, DAO, V); Vanderhoof, 5 Aug 1919, *J.M. Macoun s.n.* (CAN); Vanderhoof, 6 Aug 1919, *J.M. Macoun s.n.* (CAN, V); Pouce Coupe, 15 Jul 1921, *M.O. Malte s.n.* (CAN, DAO); Fraser Lake, 2222 ft, Aug 1922, *Mackenzie s.n.* (V); Vanderhoof, 18 Jul 1929, *S.G. Preston s.n.* (UBC); Dawson Creek, 3 Sep 1934, *H. Groh s.n.* (DAO); Smithers, Jul 1938, *J.D. Menzies s.n.* (UBC, V); Tetana Lake, 28 Jul 1938, *T. Fletcher s.n.* (V); Wardner, Aug 1939, *W.R. Foster s.n.* (UBC); Nelson, Apex, 10 Jul 1940, *J.W. Eastham 7766* (DAO, UBC); near Kinbasket Lake, 70 mi W of Golden, 21 Jul 1941, *J.W. Eastham 9296* (DAO); Kinbasket Lake, Big Bend Highway, 21 Jul 1941, *J.W. Eastham s.n.* (DAO, UBC, V); near Griffin Lake, between Revelstoke and Sicamous, 23 Jul 1941, *J.W. Eastham 9353* (DAO, UBC); Griffin Lake, 27 Jul 1941, *J.W. Eastham s.n.* (V); Alaska Highway, Minaker River, mile 157, 19 Jun 1943, *C.H.D. Clarke 4* (CAN); old Cranbrook-Moyie road, 6 Aug 1943, *J.W. Eastham s.n.* (UBC, V); vicinity of Buckinghorse River, 31 Aug 1943, *H.M. Raup & D.S. Correll 11598* (UBC); S of Hazelton, 12 Jul 1944, *J.W. Eastham s.n.* (UBC); Woodpecker at Meadow Creek, 18 Jul 1944, *J.W. Eastham s.n.* (V); Cariboo, Horsefly district, 31 Jul 1944, *J.W. Eastham s.n.* (UBC, V); Anahim Lake, Chilcotin, Aug 1944, *C.F. Cornwall 12362* (CAN, DAO, UBC, V); Smithers, 26 Jul 1946, *J.W. Eastham s.n.* (UBC); Smithers, 26 Jul 1946, *J.W. Eastham 14838* (DAO); Fort St. John, 4 Sep 1946, *H. Groh 3049* (DAO); Liard Hot Springs, 1 Aug 1946, *J.P. Anderson 10362* (CAN); vicinity of hot spring near lower crossing of Liard River, 25 Aug 1948, *H.M. Raup & D.S. Correll 11519* (CAN, UBC); Deka Lake, 4 Sep 1953, *V.C. Brink s.n.* (UBC); 1.5 mi S of Hixon along highway from Prince George to Quesnel, 10 Aug 1954, *J.A. Calder, D.B.O. Savile & J.M. Ferguson 14341* (DAO); 7 mi SW of Telkwa along Goathorn Creek, Smithers area, 31 Aug 1954, *J.A. Calder, D.B.O. Savile & J.M. Ferguson 15271* (DAO); 1 mi W of Fairy Creek, Fernie, 3500 ft, 31 Jul 1956, *F.J. Hermann 13014* (US); Kootenay National Park, McCleod Meadows, 2 mi S along Nixon Creek, 3700 ft, 9 Aug 1956, *F.J. Hermann 13227* (US); 5.5 mi E of Bridge Lake P.O. on road to Littlefort, 11 Aug 1956, *J.A. Calder, J. A. Parmelee & R.L. Taylor20007* (DAO); 1 mi W of McClinchy Creek bridge between Kleena Kleene and Anahim Lake, W of Williams Lake, 15 Aug 1956, *J.A. Calder, J. A. Parmelee & R.L. Taylor 20122* (DAO); Sage Creek Lodge, Flathead, 5100 ft, 22 Jul 1957, *J. Davidson s.n.* (DAO, UBC, V); Help Lake area 24 mi NW of Donald, 8 Aug 1958, *R.L. Taylor & D.H. Ferguson 3654* (DAO); Liard Hot Springs, ca.1300 ft, 28 Jun 1960, *A.E. Porsild & R.T. Porsild 21954* (CAN); Liard Hotsprings, 27 Jul 1960, *J.A. Calder & I. Kukkonen 27556* (DAO); Wells Gray Provincial Park, outside the park boundary at the S entrance, near Hemp Creek Ranger Station, S Cariboo Mountains, 9 Jul 1961, *L. Ahti & T. Ahti 6877* (DAO); point of land overlooking Peace River Valley, 25 mi W of Fort St. John, last

week of Jul 1961, *D. Kyanston & M.S. Dhaliwal 7* (DAO); Willow River, 20 mi S of Giscome, 10 Aug 1963, *S. Eis & A. Auclair 451* (CAN); 4 mi N of Davie Lake, ca. 50 mi N of Prince George, 16 Aug 1963, *A. Auclair 484* (DAO); Prince George District, along the road to Davie Lake, 2000–2400 ft, 17 Aug 1963, *A. Auclair & S. Eis s.n.* (DAO); Portage Mtn dam, 25 Jul 1965, *A. F. Szczawinski 7/65* (V); N of Williams Lake, 11 Jul 1967, *C. Beil 67-7-11-14* (UBC); Murray Range NE of Pine Pass, Cariboo District, 19 Jul 1971, *R. Revel s.n.* (UBC); Glacier National Park, Mountain Creek Campground, 29 Jul 1972, *E. Haber & M.J. Shchepanek 1698* (CAN); Manning Park, Orchid meadow, 2 mi E of Ranger Station, 31 Jul 1973, *C. C. Chuang 870, 880* (CAN); Taspai Creek, ca. 27 mi ESE of Prince George, 2550 ft, 5 Aug 1974, *V.J. Krajina, J. Pojar & C. Parsons s.n.* (UBC); Jim Meadow, Chilcotin, 24 Jul 1979, *C. Selby & A. Roberts s.n.* (UBC); near Cooper Creek, 1340 m, 20 Aug 1980, *L.E. Pavlick 80-560* (V); Cariboo District, near Ratdam, N of Horsefly, 16 Jul 1982, *S.G. Aiken & S.J. Darbyshire 2350* (DAO); Upper Teslin River, 8 Aug 1983, *C. McEwen 6207* (DAO); Chilcotin area, Cooper Creek, junction of road to Lake Mons and Sky ranch, 14 Sep 1993, *J. Cayouette 7615* (DAO); Peace River Land District, 6 km N of Chetwind, 10 Sep 1998, *J. Cayouette 8494* (DAO); Cariboo Land District, Perry Road, S of Shelley, 11 Sep 1998, *J. Cayouette 8495* (DAO); Cariboo Land District, Dome Creek, road 16, 11 Sep 1998, *J. Cayouette 8497* (DAO); Mount Robson Prov. Park, Redpass, close to Fraser River, 11 Sep 1998, *J. Cayouette 8499* (DAO); Willow Creek Rest Area on Hwy 16, S of Prince George, 6 Jul 2004, *P.M. Peterson, J.M. Saarela & S. Smith 18446* (CAN, US); Liard River Hot Springs Provincial Park, 20 Jul 2004, *P.M. Peterson, J.M. Saarela & S. Smith 18659* (CAN, UBC).

3. Bromus commutatus Schrad., Fl. Germ. 353. 1806. (**Figs. 3C, 4A–D**). *Brachypodium commutatum* (Schrad.) P. Beauv., Ess. Agrostogr. 101, 155. 1812. *Bromus mutabilis* var. *commutatus* (Schrad.) F.W. Schultz, Flora 32:234. 1849. *Serrafulcus commutatus* (Schrad.) Bab., Man. Brit. Bot. 1:374. 1843. *Bromus racemosus* var. *commutatus* (Schrad.) Coss. & T. Durand, Expl. Sci. Algérie 2:165. 1855. *Bromus mollis* var. *commutatus* (Schrad.) Sanio, Verh. Bot. Vereins Prov. Brandenburg 23:Abh. (3)31. 1882. *Serrafulcus racemosus* var. *commutatus* (Schrad.) Husn., Graminees 72. 1899. *Forasaccus commutatus* (Schrad.) Bubani, Fl. Pyren. 4:387. 1901. *Bromus racemosus* subsp. *commutatus* (Schrad.) Tourlet, Cat. Pl. Vasc. Indre-et-Loire 588. 1908. *Bromus hordeaceus* var. *commutatus* (Schrad.) Fiori, Nuov. Fl. Italia 1:149. 1923. *Bromus secalinus* subsp. *commutatus* (Schrad.) Lloret, Collect. Bot. (Barcelona) 22:151. 1993. Type: GERMANY: Inter segetes, ad vias, sepes, alibique.

Bromus secalinus var. *gladewitzii* Farw., Amer. Midl. Naturalist 10:24. 1926. Type: U.S.A. Michigan: Edgewater Park, *Farwell & Gladewitz 7434* (isotype: MICH-1108616).

Annual; rhizomes absent; plants 20–100 cm tall. Culms 1.5–3 mm wide at base, smooth; nodes 3–5, yellow-brown, densely pubescent with stiff hairs 0.2–1 mm long. Leaf sheaths closed for most of their length, densely pubescent, hairs soft and wavy to 1.2 mm long; auricles absent; ligules 1–3 mm long, membranous, glabrous or pubescent, erose; blades 8–16 cm long, 2–4 mm wide, adaxial surface densely pubescent with long, stiff hairs to 2.5 mm long, abaxial surface pubescent with dense hairs 0.1–0.5 mm long, margins smooth or serrulate. Panicles 5.5–17 cm long, 2.5–8 cm wide, open, longest lower branch > 4 cm long (as measured from node to apex of terminal floret including awn); branches erect to ascending, sometimes secund, scabrous to pubescent, 1–3 spikelets per branch, lowest inflorescence node with 1–3 branches. Spikelets 2–3 cm long (including awns), ovate-lanceolate, rachillas sometimes visible at maturity, florets 6–12. Glumes slightly subequal, smooth or scabrous, keels occasionally serrulate distally; lower glumes 5.5–8.2 mm long, 5-nerved; upper glumes 6.9–8.5 mm long, 7(9)-nerved. Lemmas 7–11 mm long, 1.5–2 mm wide, 7–9-nerved, nerves visible but not conspicuously raised, backs glabrous or scabrous to puberulent, margins often bluntly angled, apex entire or minutely bifid, the cleft 0.1–0.2 mm deep; awns 5–8.5 mm long, arising < 1.5 mm below lemma apex, straight or minutely divaricate, antrorsely scabrous, awn of lowest floret shorter than others. Paleas 6-10 mm long, shorter than lemmas, backs glabrous, keels ciliate, cilia to 0.3 mm long. Stamens 2; anthers 0.5–2.5 mm long, dark brown. $2n$ = 14, 28, 56.

Distribution and Habitat.—Introduced. *Bromus commutatus* is native to Europe. It is common in eastern and western North America and occurs in scattered locations across the United States Great Plains (Pavlick & Anderton 2007). In British Columbia, *B. commutatus* occurs in the southern portion of the province (Fig. 3C). Habitats include waste places, fields and grasslands. Elevation: 0–967 m.

Common Names.—English: hairy brome, hairy chess, meadow brome, upright chess; French: brome variable, brome confondu.

Notes.—*Bromus commutatus* and *B. racemosus* are morphologically similar species that are often notoriously difficult to distinguish. They are both native to Europe, but now much more widely distributed. Hitchcock & Chase (1951:49) noted that these taxa are "differentiated only by arbitrary characters." In his classification of subgenus *Bromus* (=*B.* sect. *Bromus*), Scholz (1970) placed *B. commutatus* and *B. racemosus* in different series, and many authors recognize them as separate species (e.g., Clapham et al. 1987; Conert 1997; Smith

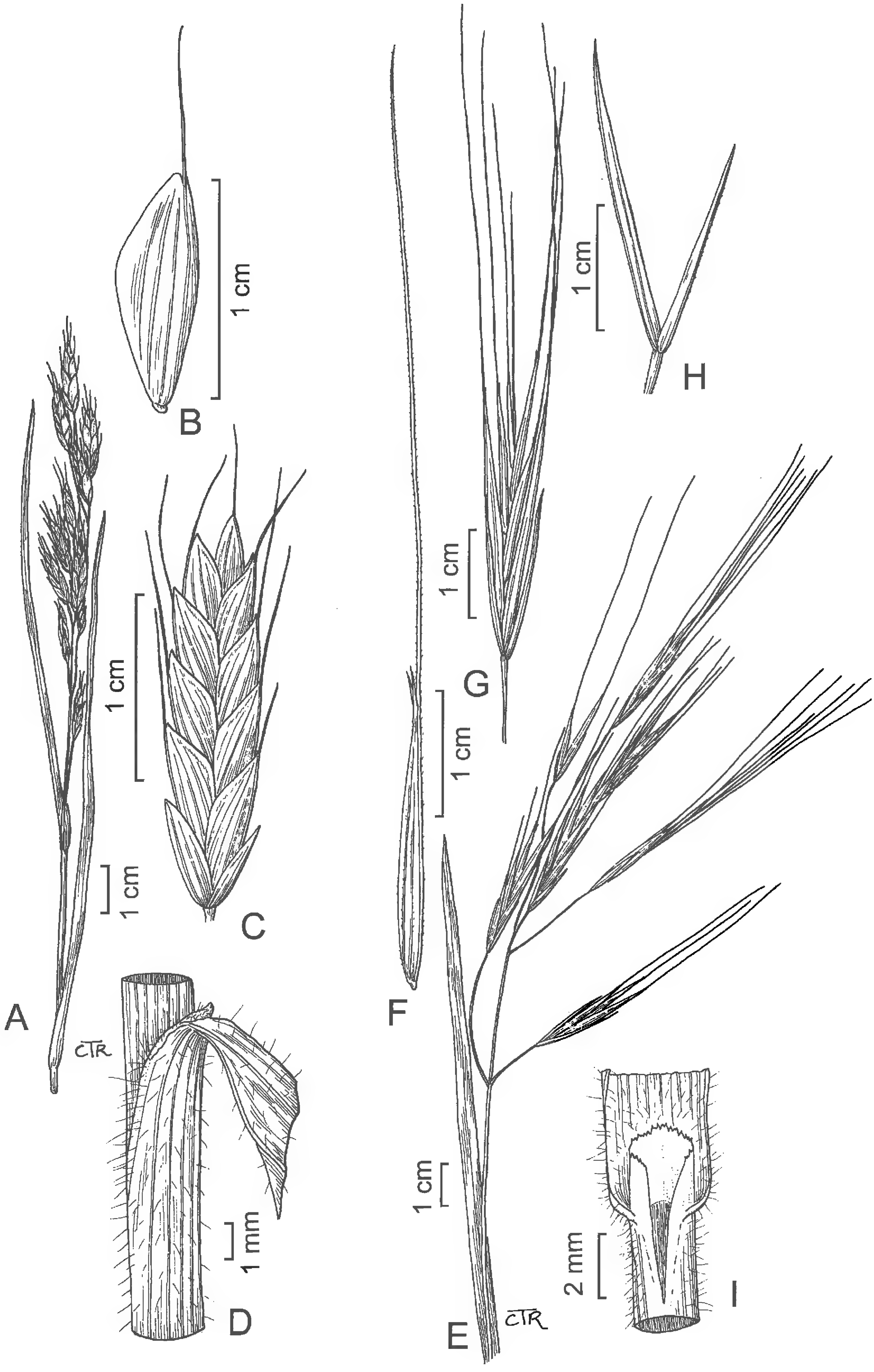

FIG. 4. *Bromus commutatus*. A. Inflorescence. B. Lemma. C. Spikelet. D. Ligule. *Bromus diandrus*. E. Inflorescence. F. Floret. G. Spikelet. H. Glumes. I. Ligule.

1980, 1985; Stace 1997; Douglas et al. 2001; Pavlick & Anderton 2007; Saarela & Peterson in press), but others have treated *B. commutatus* as a subspecies of *B. racemosus* (e.g., Shear 1900; Acedo & Llamas 1999; Lauber & Wagner 1996; Meijden 1996) or at least suggested that this treatment might be appropriate (e.g., Pavlick 1995; Planchuelo & Peterson 2000). Some workers lump these taxa and recognize only a single, variable species (e.g., Liang et al. 2006). Acedo & Llamas (1999) noted substantial morphological variation among these taxa in the Iberian Peninsula, and indicated that environmental conditions influence plant and inflorescence size.

In most treatments, *B. commutatus* is circumscribed as having longer lemmas (8–11 mm vs. 6.5–8 mm in *B. racemosus*), broadly angled lemma margins (vs. rounded) and shorter anthers (but measurements in earlier keys vary substantially) [reviewed by Spalton 2002]. Additionally, *B. commutatus* is generally considered to have more open panicles with longer branches that sometimes have more than one spikelet (vs. less open panicles with shorter branches usually with a single spikelet), but these characters have not often been used in keys. Spalton (2002) conducted a morphological analysis of *B. racemosus*, *B. commutatus* and the morphologically similar species *B. secalinus*, based on material from throughout their native ranges. He demonstrated substantial overlap in characters traditionally used to distinguish *B. racemosus* and *B. commutatus* (e.g., lemma length) and found that the single best diagnostic character to distinguish the taxa is the length of the lowest panicle branches (including the terminal spikelet) (i.e., > 4 cm long in *B. commutatus* vs. < 4 cm long in *B. racemosus*). Consequently, Spalton's (2002) circumscriptions of *B. commutatus* and *B. racemosus* are slightly different from those employed by earlier authors, but his work is also the most comprehensive study of variation in the complex. Spalton (2002) concluded that *B. commutatus* is distinguished by its larger, more open and often branched inflorescences and larger spikelets, and *B. racemosus* is distinguished by its narrower, unbranched inflorescences and smaller spikelets. Using these characters, most British Columbia individuals can be readily placed into one of these two taxa. My observations of material from British Columbia indicate that plants with longer inflorescence branches are generally more robust, usually with some branches that have more than one spikelet and larger spikelets. I follow Spalton's circumscription here and recognize *B. commutatus* and *B. racemosus* at the species level, as in most recent treatments of these taxa in North America and Europe. I have observed mixed populations of *B. commutatus* and *B. racemosus* in British Columbia near Princeton [*Saarela, Sears & Maze 586A* (CAN, UBC), *586B* (CAN)] and Elko [*Saarela 405A* (CAN, UBC), *405B* (CAN)]. A comprehensive genetic study of this complex, ideally based on material from throughout their native ranges, would contribute to clarifying the natural boundaries between these taxa.

Representative Specimens Examined. **CANADA. British Columbia:** Cedar Hill, Vancouver Island, 16 Jun 1887, *Macoun 29982* (CAN); vicinity of Victoria, 6 Jun 1908, *J. Macoun 77852* (CAN, US); Saltspring Island, 24 May 1914, *J.M. Macoun 90094* (CAN, US); Comox, Vancouver Island, 19 Jun 1915, *J.M. Macoun 93968* (CAN); Vernon, 27 Jun 1917, *E.M. Warren s.n.* (UBC); Langley Prairie, 30 May 1931, *H. Groh s.n.* (DAO); S bank of Fraser River, N Ladner, 7.5.1932, *E.P. Hume s.n.* (UBC); Sumas Recreation, 13 May 1935, *D.W. Thompson s.n.* (UBC); Victoria, 2 Jun 1938, *J.W. Eastham s.n.* (UBC); Creston, 21 Jun 1938, *J.W. Eastham s.n.* (UBC); The Gorge, Victoria, 11 Jun 1939, *J.W. Eastham s.n.* (DAO, UBC); Sproat River Falls, 1 Jul 1939, *J.W. Eastham s.n.* (UBC); Arrowhead, 19 Jul 1939, *H. Groh 210* (DAO); S of Kamloops, 24 Jul 1939, *H. Groh 29.5* (DAO); Christine Lake, 16 Jun 1940, *J.W. Eastham s.n.* (UBC); Thetis Lake, 27 May 1941, *J.W. Eastham s.n.* (UBC); Cariboo District, Alkali Lake, 640 m, 18 Jul 1982, *S.G. Aiken, S.J. Darbyshire & A. Roberts 2396* (DAO); Abbotsford, intersection of Hwys. 1 and 11, along ramp, 29 Jun 1988, *S.J. Darbyshire 3729* (CAN); Great Northern Way near Clarke Drive, Vancouver, 22 Jun 1994, *F. Lomer 94-251* (UBC); Kettle River Campground, 5 km N of jct. 3 and 33 along Hwy 33, 25 Jun 2003, *J.M. Saarela & A. Roe 254* (CAN, UBC); Rocky Mountain Forest District, along Hwy 3, 1.5 km E of Elko, 23 May 2006, *J.M. Saarela 405B* (CAN); 10 km W of Princeton on Hwy 3, 19 Jun 2006, *J.M. Saarela, C. Sears & J. Maze 586B* (CAN); NE of Osoyoos ca. 3 km going up Anarchist Mountain, just before town lookout and just beyond the first switchback, 20 Jun 2006, *J.M. Saarela, C. Sears & J. Maze 644* (CAN, UBC); W of Osoyoos, 1.3 km up Richter Mountain Road, 19 Jun 2006, *J.M. Saarela, C. Sears & J. Maze 631* (CAN, UBC); Fairview Road, ca. 2 km NE from intersection with Lowe Road, Blind Creek Indian Reserve, NE of Cawston, 19 Jun 2006, *J.M. Saarela, C. Sears & J. Maze 619* (CAN, UBC); Spotted Lake, ca. 5km W of Osoyoos, S of Hwy 3, 20 Jun 2006, *J.M. Saarela, C. Sears & J. Maze 679* (CAN).

4. Bromus diandrus Roth, Bot. Abh. Beobacht. 44. 1787. (**Figs. 4E–I, 5A**). *Anisantha diandra* (Roth) Tutin, Fl. British Isles, ed. 2. 1149. 1962. *Anisantha diandra* (Roth) Tutin ex Tzvelev, Bot. Mater. Gerb. Bot. Inst. Acad. Nauk SSSR 22:4. 1963. Type: Gr. Bromoides, locustis maximus, lanuginosum, Italicum, Hist. Nat. 261. no. 444 (neotype: OXF-Scheuchzer herb., designated by Sales, Edinb. J. Bot. 50:8. 1993).

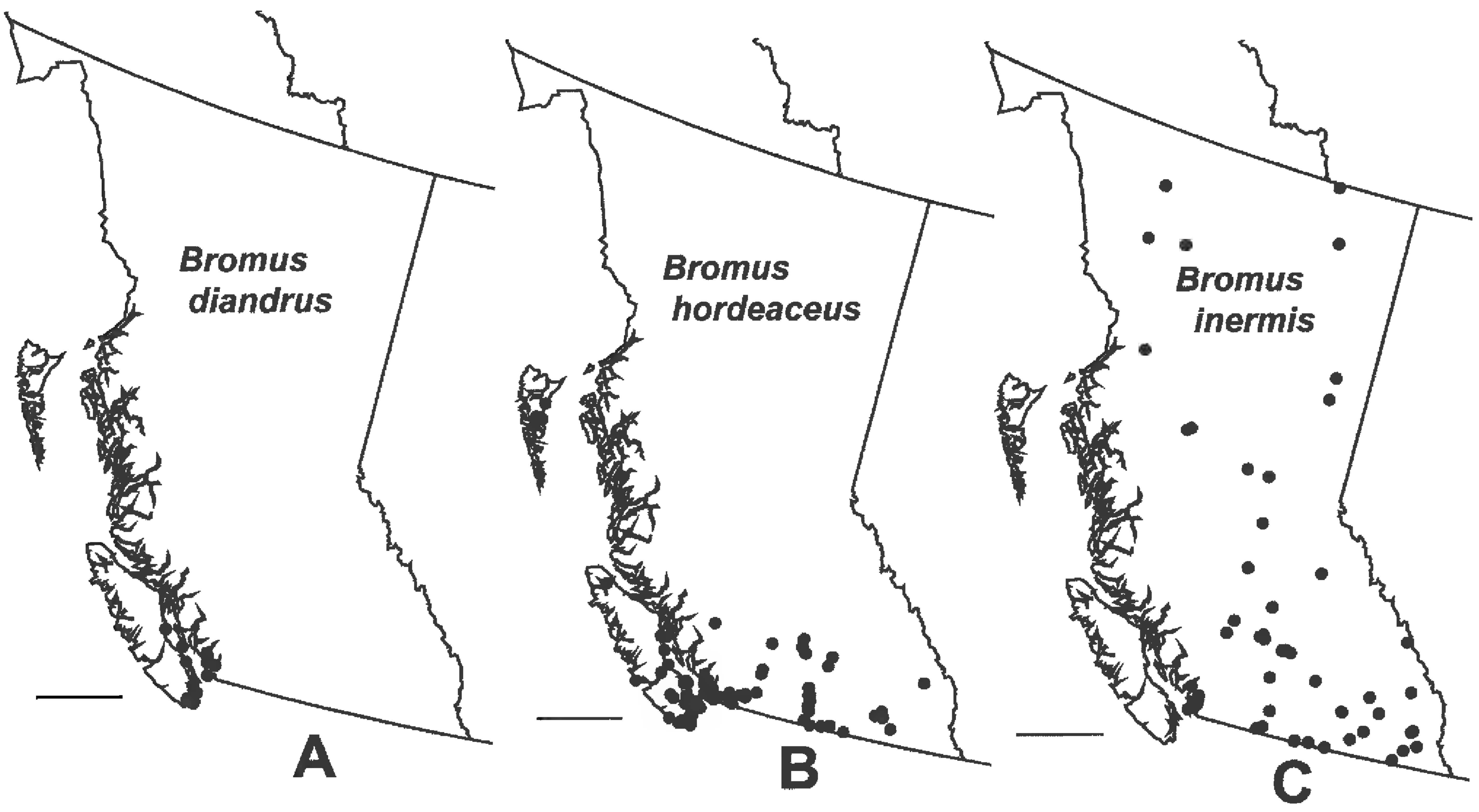

Fig. 5. Geographic distribution in British Columbia. A. *Bromus diandrus*. B. *Bromus hordeaceus*. C. *Bromus inermis*. Scale bars = 200 km.

Bromus rigidus Roth, Bot. Mag. (Römer & Usteri) 10:21–23. 1790. *Genea rigida* (Roth) Dumort., Étude Michelaria 30. 1868. *Bromus madritensis* var. *rigidus* (Roth) Bab. ex Syme, Engl. Bot., ed. 3b. 11:161. 1873. *B. villosus* var. *rigidus* (Roth) Asch. & Graebn., Syn. Mitteleur. Fl. 2:595. 1901. *Anisantha rigida* (Roth) Hyl. Uppsala Univ. Arsskr. 7:32. 1945. *Bromus diandrus* subsp. *rigidus* (Roth) Lainz, Aanl. Inst. Forest. Invest. Exper. 12:49. 1967. *Anisantha diandra* Roth subsp. *rigida* (Roth) Tzvel., Zlaki SSSR. 1:223. 1976. *Bromus diandrus* subsp. *rigidus* (Roth) O. Bolòs, Masalles & Vigo, Collect. Bot. (Barcelona) 17:96. 1987[1988]. *Bromus diandrus* var. *rigidus* (Roth) Sales, Edinb. J. Bot. 50:9. 1993. Type: Habitat in Europa australi (neotype: B-Willd., designated by Sales, Edinb. J. Bot. 50:9–10. 1993).

Annual; rhizomes absent; 15–120 cm tall. Culms 0.8–3 mm wide at base, smooth, sometimes pubescent below panicles; nodes 2–3, blackish brown, glabrous. Leaf sheaths closed for most of their length, pubescent, with short stiff hairs to 0.6 mm long or soft hairs to 2.5 mm long; auricles absent; ligules 2.2–5 mm long, membranous, glabrous, erose-lacerate; blades 3–18 cm long, 2–7 mm wide; adaxial and abaxial surfaces pubescent with long, soft hairs to 1.5 mm long, margins smooth or hairy. Panicles 6–30 cm long, 2–25 cm wide, erect when young, sometimes becoming spreading or nodding at maturity; branches usually shorter than spikelets, scabrous to densely pubescent, usually with one spikelet per branch; lowest inflorescence node with 1–3 branches. Spikelets 6.5–8 cm long (including awns), cuneate, ±compressed dorsiventrally, sometimes spreading at maturity with visible rachillas; florets 5–8. Glumes subequal, linear-lanceolate, glabrous, keels glabrous or serrulate, particularly distally, margins hyaline; lower glumes 12–26 mm long, 1(–3)-nerved; upper glumes 18–35 mm long, 3(–5)-nerved. Lemmas 18–35 mm long, 1–2 mm wide, 7-nerved, lanceolate, backs sparsely to densely scabrous, sometimes with hairs to 1 mm long at apex or along margins, occasionally with a dense tuft of hairs 0.1–0.2 mm long at base, margins hyaline (except at base), smooth or minutely serrulate, keels serrulate, apex bifid, the cleft 2.2–5.2 mm deep; awns 30–50 mm long, arising 3.5–6 mm below lemma apex, straight, antrorsely scabrous. Paleas 13–16 mm long, shorter than lemmas, backs glabrous, keels ciliate, cilia to 0.5 mm long. Stamens 3; anthers 0.5–1.2 mm long, dark brown. $2n$ = 42, 56.

Distribution and Habitat.—Introduced. *Bromus diandrus* is native to Europe. In North America it is common in the west from Washington to California and Texas, with some scattered localities in the southeastern United States (Pavlick & Anderton 2007). In British Columbia the species occurs on southern Vancouver Island and in the Vancouver area (Fig. 5A), where it is distributed in waste places, roadsides, thickets, river banks, sand bars, rocky outcrops, grassy banks and disturbed ground. Elevation: 0–290 m.

Common Names.—ripgut brome, ripgut grass.

Notes.—In British Columbia (Douglas et al. 2001) and elsewhere in western North America, this introduced taxon has previously been treated as *B. rigidus* Roth. Sales (1993) conducted a comprehensive survey of morphological, geographical and ecological variation in the *Bromus diandrus/ rigidus* complex based on material collected throughout its native European range, and recognized these taxa as varieties: *B. diandrus* var. *diandrus* and *B. diandrus* var. *rigidus* (Roth) Sales. However, Sales (1993) noted that the differences between her varieties are very subtle and that it is often very difficult to place specimens into one variety or the other. I therefore treat all British Columbia material as *B. diandrus* s.l., with no recognition of intraspecific taxa, as in the recent *Bromus* treatment for North America by Pavlick and Anderton (2007) and that forthcoming for California (Saarela & Peterson in press). *Bromus diandrus* has the largest spikelet characters (glumes, lemmas, awns) among the three *B.* sect. *Genea* species in British Columbia; consequently, it is straightforward to identify.

Representative Specimens Examined. **CANADA. British Columbia:** near Victoria, Jun 1876, *Dawson 30040* (CAN); Nanaimo, Vancouver Island, 12 Jul 1893, *Macoun 30039* (CAN); Nanaimo, Vancouver Island, 17 Jul 1908, *J. Macoun 76832* (CAN, US); Victoria, 17 Aug 1912, *M.O. Malte 108314* (CAN, DAO); vicinity of Sidney, 20 Jun 1913, *J. Macoun 88538* (CAN); Victoria, 1 Jun 1938, *J.W. Eastham 419c* (UBC); C. N. railway yards, Nanaimo, Vancouver Island, 31 May 1939, *J.W. Eastham s.n.* (DAO); Vancouver Island, Anderson Hill, near Victoria, 65 m, 17 May 1950, *V. Krajina & R.H. Spilsbury 3859* (DAO); Victoria, above McNeil Bay, 60 m, 21 May 1950, *V. Krajina & R.H. Spilsbury 3950* (UBC); Nanaimo, Vancouver Island, 10 m, 12 Jun 1950, *V. Krajina, R.H. Spilsbury & A. Szczawinski 9360* (DAO, UBC); Esquimalt Lagoon, Victoria, 3 May 1962, *J. Spraggs s.n.* (DAO); Esquimalt Lagoon near Victoria, 29 May 1962, *J. Hett s.n.* (DAO [3 sheets]); Victoria and vicinity, Vancouver Island, 10 Jul 1964, *H.J. Scoggan 15431* (CAN); Gonzales Hill, Vancouver Island, 300 ft, 14 May 1965, *B.W. Davies & R.A. Keller 365* (DAO); Smugglers Cove, Ten Mile Point, 10 ft, 19 May 1965, *B.W. Davies 446* (DAO); Goldstream Park, Victoria, 20 Jul 1980, *R. Hainault 8244* (DAO); Vancouver Island, S Saanich District, Saanich Peninsula, Central Saanich Municipality, Island View Beach, Cordova Spit, 2 Jul 1982, *S.G. Aiken, S.J. Darbyshire & L.E. Pavlick 2127* (DAO); Cowichan District, Saltspring Island, Mount Tuam above Cape Keppel, 950 ft, 3 Jul 1982, *S.G. Aiken, S.J. Darbyshire & L.E. Pavlick 2154* (DAO); Goose Spit, Comox, 4 May 1984, *V.C. Brink s.n.* (UBC); Sangster Island, 20 May 1985, *A. Ceska, O. Ceska & M. Ceska s.n.* (UBC); Holland Point, Victoria, 30 Jun 1988, *S.J. Darbyshire 3737* (CAN, DAO); Cadboro Bay, Victoria, 1 Jul 1988, *S.J. Darbyshire 3747* (CAN, DAO); University of British Columbia, Museum of Anthropology, edge of parking lot, 15 May 2006, *J.M. Saarela 332* (CAN, UBC); Horseshoe Bay, Whytecliff Park, 27 May 2006, *J.M. Saarela 509* (CAN, UBC); S end of Tsawassen Drive S, Tsawassen Indian Reserve #0, 28 May 2006, *J.M. Saarela & C. Sears 544* (CAN, UBC); Vancouver Island, Island View Park, S of Hwy 17 between Sidney and Victoria, 4 Jun 2007, *J.M. Saarela, D.M. Percy & Y. Chang 847* (CAN, UBC).

5. Bromus hordeaceus L., Sp. Pl. 1:77. 1753. (**Figs. 5B, 6**). *Bromus secalinus* var. *hordeaceus* (L.) L., Flora Suecica, ed. 2. 90. 1755. *Bromus mollis* var. *hordeaceus* (L.) Fries, Novit. Fl. Suec. 16. 1814-23. *Bromus mollis* subsp. *hordeaceus* (L.) Hiitonen, Suom. Kasvio 219. 1933. Type: EUROPE: in collibus aridissimis sabulosis. (Lectotype: [icon] *"Gramen avenaceum pratense, gluma breviore squamosa et villosa"* in Morison, Pl. Hist. Univ. 3: s. 8, pl. 7, f. 18. 1699, designated by Smith in Cafferty et al., Taxon 49:248. 2000; Epitype: LINN-93.7, designated by Smith in Cafferty et al., Taxon 49:248).

Bromus mollis L., Sp. Pl., ed. 2. 112. 1762. *Serrafulcus mollis* (L.) Parl., Pl. Rar. Sic. 2:11. 1840. *Forasaccus mollis* (L.) Bubani, Fl. Pyr. 4:386. 1901. *Bromus hordeaceus* var. *mollis* (L.) Fiori, Nuov. Fl. Italia. 1:149. 1923. *Bromus hordeaceus* subsp. *mollis* (L.) Maire, Cat. Pl. Maroc. 4:943. 1941. Type: EUROPE: in australioris siccis (Lectotype: LINN-93.6, designated by Smith in Cafferty et al., Taxon 49:248. 2000).

Annual; rhizomes absent; plants 7–110 cm tall. Culms 0.8–5 mm wide at base, smooth; nodes 2–4, yellow-brown, minutely to densely pubescent, hairs soft or stiff, to 0.6 mm long. Leaf sheaths closed for most of their length, moderately to densely pilose, hairs soft and wavy to 1.2 mm long; auricles absent; ligules 1–2.6 mm long, membranous, glabrous or pubescent, erose; blades 2.2–18 cm long, 1–5.3 mm wide, adaxial surface densely pubescent with long, stiff hairs to 1.2 mm long, abaxial surface pubescent with dense hairs to 0.3 mm long or like adaxial surface, margins smooth or serrulate. Panicles 2.5–14 cm long, 1–4 cm wide, dense, sometimes reduced to a single spikelet; branches erect to ascending or somewhat lax, scabrous to pubescent, most shorter than spikelets, 1 spikelet per branch; lowest inflorescence node with 1–3 branches. Spikelets 1.7–3 cm long (including awns), ovate-lanceolate, rachillas sometimes visible at maturity, florets 6–11. Glumes subequal, minutely to densely pubescent, keels serrulate; lower glumes 5.2–7 mm long, 3–5-nerved; upper glumes 6–8.5 mm long, 7–9-nerved. Lemmas 7.5–9 mm long, 1.9–2.5 mm wide, 7–9-nerved, nerves visible and conspicuously raised, particularly apically, backs densely pubescent with hairs to 0.3 mm long,

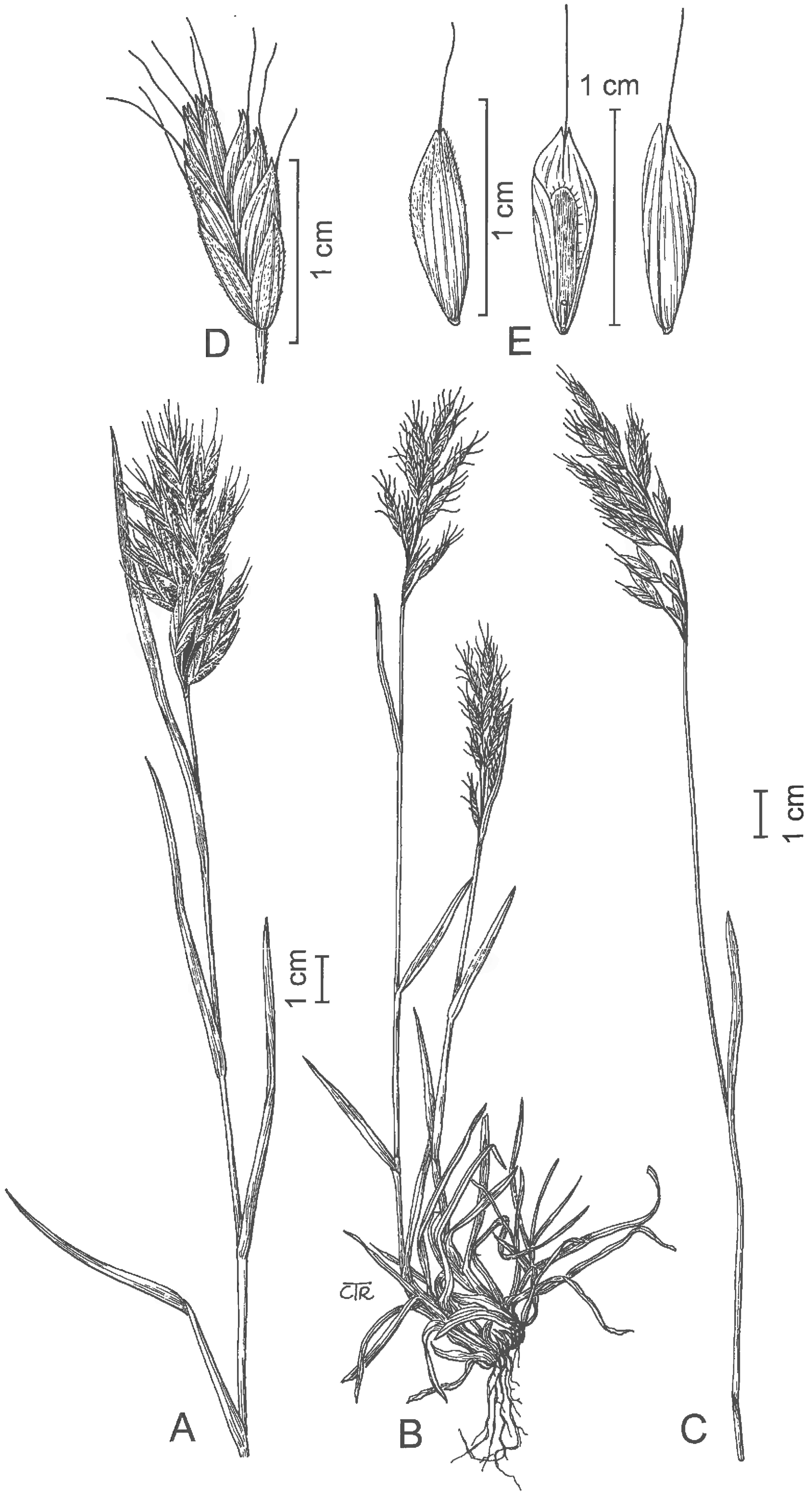

FIG. 6. ***Bromus hordeaceus***. A, B, C. Habit. D. Spikelet. E. Lemmas.

hyaline margins 0.3–0.6 mm wide, often bluntly angled; apex bifid, the cleft 0.3–0.7 mm deep; awns 4–7.6 mm long, arising 0.4–1.2 mm below lemma apex, straight or slightly divaricate, antrorsely scabrous. Paleas shorter than lemmas, backs glabrous, keels ciliate, cilia to 0.3 mm long. Stamens 2; anthers 0.3–1.3 mm long, dark brown. $2n = 28$.

Distribution and Habitat.—Introduced. *Bromus hordeaceus* is thought to be native to the Meditteranean basin (Smith 1986). It is now distributed widely in North America (Pavlick & Anderton 2007), Europe, Africa and Australia. In British Columbia *B. hordeaceus* occurs throughout the southern portion of the province and on the Queen Charlotte Islands (Fig. 5B). It is distributed in waste places, roadsides, fields, grassy areas and sandy beaches. Elevation: 0–1110 m.

Common Names.—English: soft chess, soft brome-grass, soft cheat, tender brome-grass, soft-brome, soft brome; French: brome mou, brome doux, brome mollet.

Notes.—*Bromus hordeaceus* can be very difficult to distinguish from *B. racemosus*, even with considerable experience. These taxa have been lumped by some workers, reflecting this difficulty (e.g., Wilken & Painter 1993), but most workers recognize both taxa. Their major distinguishing characteristic is the degree of lemma nerve protrusion. In *B. hordeaceus*, the lemma nerves are raised and conspicuous (Fig. 7B), whereas in *B. racemosus* the lemmas are smooth, with nerves raised barely or not at all (Fig. 7A). This character is usually most easily observed near the apex of the lemma. *Bromus hordeaceus* tends to have more dense inflorescences compared with *B. racemosus*, but there is variation in this character and it is not always reliable.

Bromus hordeaceus is a morphologically variable species (Fig. 6). In Europe, most workers recognize several intraspecific taxa (as subspecies) in the complex, differentiated by lemma length, awn width at its base, awn curvature, culm height and spikelet pubescence (e.g., Smith 1968, 1980, 1985; Zajac 1996). These subspecies are generally difficult to tell apart, but they have been recognized in recent treatments for North America (e.g., Pavlick 1995; Pavlick & Anderton 2007). Two subspecies [subsp. *hordeaceus* and subsp. *thominei* (Hardham ex Nyman) Braun-Blanquet] were recognized in British Columbia by Douglas et al. (2001). Douglas et al. (2001) also indicated that the putative hybrid *B. x pseudothominei* P.M. Sm. (*B. hordeaceus* subsp. *hordeaceus* × *B. lepidus* Holmberg) is infrequent on southern Vancouver Island.

In material of the *B. hordeaceus* complex from British Columbia, I have observed that many individuals have a combination of the morphological characters typically used in keys to distinguish the subspecies, and they cannot be reliably differentiated. Specimens of the putative hybrid are also indistinguishable from other *B. hordeaceus* individuals. Ainouche et al. (1996, 1999) found no evidence of DNA sequence or allozyme differentiation among individuals of the putative *B. hordeaceus* subspecies collected from throughout their native eastern Meditteranean ranges, and also noted substantial overlap in morphological characters traditionally used to segregate intraspecific taxa among populations they examined. Intraspecific taxa in this group in North America are not recognized here.

Representative Specimens Examined. **CANADA. British Columbia:** Victoria, 6 Jun 1893, *Wm. Scott s.n.* (DAO); Cascade Station, near International Boundary between Kettle and Columbia rivers, 26 Jun 1902, *J.M. Macoun 63,330* (US); Armstrong, 29 Jun 1907, *E. Wilson s.n.* [?] (UBC); vicinity of Victoria, 13 Jun 1908, *J. Macoun 76853* (US); Vancouver Island, Robertson River, 5 Jul 1911, *W. Spreadborough s.n.* (CAN); Victoria, 13 Sep 1909, *A.S. Hitchcock 4863* (US); Spence's Bridge, 16 Jul 1913, *J. Davidson s.n.* (UBC); Mayne Island, 20 May 1914, *J.M. Macoun 90,077* (US); White Rock, 4 Jun 1916, *J. Davidson s.n.* (UBC); Vancouver, 10th Ave. and Willow St., Jun 1918, *J. Davidson s.n.* (UBC); Lulu Island, 15 Jun 1924, *T.R. Ashlee s.n.* (UBC); White Rock, 25 May 1924, *T.R. Ashlee s.n.* (UBC); Mante [?] Creek, June 1927, *Bostock s.n.* (DAO); Agassiz, 3 Sep 1930, *H. Groh s.n.* (DAO); Langley Prairie, 4 Sep 1930, *H. Groh s.n.* (DAO); Abbotsford, 12 Sep 1930, *H. Groh s.n.* (DAO); Sumas Prairie, 15 Sep 1930, *H. Groh s.n.* (DAO); Sooke, 6 Oct 1930, *H. Groh s.n.* (DAO); Mt Lehman, 12 May 1931, *H. Groh s.n.* (DAO); New Westminster, 19 May 1931, *H. Groh s.n.* (DAO); New Westminster, 19 May 1931, *H. Groh s.n.* (DAO); Horseshoe Bay, 23 May 1931, *H. Groh s.n.* (DAO); Saanichton, 27 May 1931, *H. Groh s.n.* (DAO); Langley Prairie, 30 May 1931, *H. Groh s.n.* (DAO); Agassiz, 2 Jun 1931, *H. Groh s.n.* (DAO); S bank of Fraser River, N Ladner, 7.5.1932, *E.P. Hume 602* (UBC); Saanichton, Vancouver Island, 24 Jun 1935, *A.M. Eastham s.n.* (UBC); Lower Fraser, 18 Jul 1935, *P.P. Henson s.n.* (DAO); Coal Harbour, 25 Jun 1936, *L.E. Taylor 2414* (UBC); Crescent Beach, 31 May 1937, *J.W. Eastham 469* (UBC); Summerland, May 1936, *V.C. Brink s.n.* (UBC); W Point Grey, Vancouver, 27 Jun 1937, *J.W. Eastham s.n.* (UBC); Nanaimo, 31 May 1939, *J.W. Eastham s.n.* (UBC); Saanichton, Jun 1939, *W.R. Foster s.n.* (DAO, UBC); Vancouver Island, Saanichton, 5 Jul 1939, *I. Mounce s.n.* (DAO); Duncan, 7 Jul 1939, *W. Newton s.n.* (DAO); Langley Prairie, 26 Jul 1939, *H. Groh 322* (DAO); Otter, 1 Aug 1939, *H. Groh 381* (DAO); Vancouver Island, Shelter Point, 5 mi N of Oyster River, 5 Aug 1939, *I. Mounce s.n.* (DAO); James Island, off Saanichton, 5 Aug 1939, *H. Groh 438* (DAO); Kamloops, Brigade Lake, 2800 ft, 24 Jul 1940,

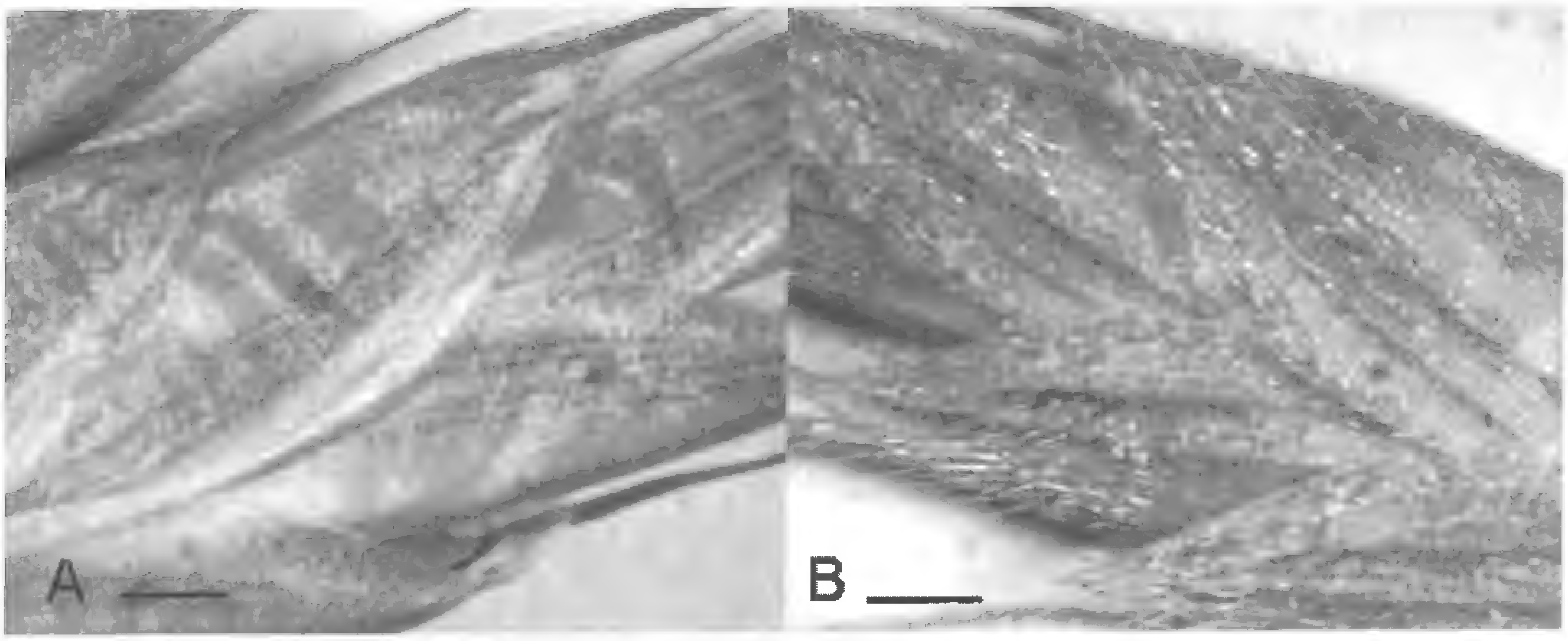

Fig. 7. Lemma morphology. A. *Bromus racemosus* [*Saarela, Sears & Maze 586A* (CAN)]. Lemma surface is smooth; nerves are not conspicuously protruding. B. *Bromus hordeaceus* [*McCalla 8256* (UBC-61258)]. Lemma surface is rough; nerves are conspicuously protruding. Scale bars = 1 mm. Note that the presence or absence of lemma pubescence is not useful in distinguishing these taxa.

E.W. Tisdale 40-7 (US); Nelson, 20 Jun 1944, *W.G. McCalla 8256* (DAO); N of Fraser River, Mission, 500 ft, 7 Aug 1949, *G.F. Ledingham 49-513* (DAO); Duncan, 19 Jul 1950, *E. G. Anderson 972* (DAO); Old W Saanich Road near Victoria, drainage of Colquitz Creek, 390 ft, 22 May 1963, *A. Young & W. Hubbard s.n.* (DAO); Gorden Head, 10 ft, 18 May 1965, *B.W. Davies 397* (DAO); Gillespie Road, East Sooke, 30 May 1965, *B.W. Davies s.n.* (DAO); Government House, Victoria, 200 ft, 7 Jun 1965, *R. A. Keller & B.W. Davies 822* (DAO); above Harrison River, 1 mi from Harrison Mills, 400 ft, 12 Jun 1974, *K.I. Beamish, J. Pinder-Moss, C. Selby, J. Pojar & E. Perkins 74063* (UBC); Long Lake Road, S of Kamloops, 24 Jul 1939, *J. Davidson s.n.* (UBC); Ladner, 14 Jul 1943, *H.D. Falls s.n.* (UBC); Snake Island, W Nanaimo, 30 May 1944, *L.E. Taylor 2296* (UBC); Locarno Park, 11 Jun 1944, *J.W. Eastham s.n.* (DAO); Nelson, 20 Jun 1944, *W. C. McCalla 8256* (UBC); Nelson, 21 Jun 1944, *W.C. McCalla 8267* (UBC); Hastings Park, Vancouver, 8 Jun 1923, *T.R. Ashlee s.n.* (UBC); #3 Hwy W of Nelson, 23 Jun 1944, *W.C. McCalla 8280* (UBC); edge of Hwy 3, 6 mi W of Nelson, 20 Jun 1944, *W.C. McCalla 8256* (DAO); Gray Creek, 27 Jun 1944, *W.C. McCalla 8308* (UBC); Fairfield Island, Chilliwack, 10 Jun 1946, *J.W. Eastham s.n.* (UBC); Victoria, above McNeil Bay, 60 m, 21 May 1950, *V. Krajina & R.H. Spilsbury 3946* (UBC); Bear-Cowichan Lakes, 270 m, 28 May 1950, *V. Krajina & R.H. Spilsbury 4096* (UBC); Quinsam Lake, Comox, 1 Jun 1951, *J. Bendell s.n.* (UBC); Gully at W Summerland on W side of Okanagan Lake, 27 Jun 1953, *J.A. Calder & D.B.O. Savile 9711* (DAO); along highway on W side of Skaha Lake between Penticton and Kaleden, 28 Jun 1953, *J.A. Calder & D.B.O. Savile 9784* (DAO); Goose Lake about 3 mi N of Vernon, 6 Jul 1953, *J.A. Calder & D.B.O. Savile 10145B* (DAO); 5 mi W of Ross Creek along the highway, 3100 ft, 29 Aug 1953, *V.J. Krajina s.n.* (UBC); Port Alberni, 17 May 1955, *D.R. Lindsay & W. Woodbury 658* (DAO); Christina Lake, 31 May 1954, *W.G. Dore & M. Smith s.n.* (DAO); Boston Bar, 30 May 1955, *D.R. Lindsay & W. Woodbury 862* (DAO); Saltspring Island, islet off Beaver Point, 9 Jul 1955, *T.R. Ashlee s.n.* (UBC); Deadwood Creek area, Nanaimo River Valley, 840 ft, 22 Jun 1956, *D. Mueller-Dombois 90-3* (UBC); Queen Charlotte Islands, Graham Island, Queen Charlotte City, 29 Jul 1957, *J.A. Calder, D.B.O. Savile & R.L. Taylor 23000* (DAO, UBC); Moresby Island, just S of Sandspit along road to Copper Bay, 5 Aug 1957, *J.A. Calder, D.B.O. Savile & R.L. Taylor 23207* (DAO); W Vancouver, sea level, 27 May 1960, *K. Beamish & F. Vrugtman 60501* (UBC); Java Rocks, Saturna Island, 8 Jun 1961, *T.R. Ashlee s.n.* (DAO); 100 yds W of entrance to Johnstone Creek campsite W of Rock Creek on Hwy 3, 15 Jun 1961, *G. Beke 61-81* (DAO); Happy Valley near Victoria, 30 May 1962, *J. Hett s.n.* (DAO); Queen Charlotte Islands, Graham Island, S end of Richardson Ranch at Tlell, 4 Jun 1964, *J.A. Calder, R.L. Taylor & L.C. Sherk 34658* (DAO, UBC); 2 mi E of Queen Charlotte City, Graham Island, 8 Jun 1964, *J.A. Calder, R.L. Taylor & L C. Sherk 34872* (DAO); S of Richardson Ranch farmstead, Tlell, Graham Island, 14 Jul 1964, *J.A. Calder & R.L. Taylor 35920* (DAO); Moresby Island, just S of Sandspit near radio tower on road to Copper Bay, 18 Jun 1964, *J.A. Calder & R.L. Taylor 35166* (DAO); Lawn Point N of Skidegate Mission, Graham Island, 24 Jun 1964, *J.A. Calder & R.L. Taylor 35445* (DAO); Smugglers Cove, Ten Mile Point, 10 ft, 19 May 1965, *B.W. Davies 448* (DAO); Esquimalt Lagoon, 1 Jun 1965, *B.W. Davies & R.A. Keller 699* (DAO); Rocky Point, 100 ft, 8 Jun 1965, *B.W. Davies & R.A. Keller 844* (DAO); Ten Mile Point area, 20 ft, 20 May 1965, *B.W. Davies 482* (DAO); Lock Bay, Gabriola Island, 4 Jul 1965, *K. Wade 65-57* (UBC); near Harling Point below Gonzales Hill, Victoria, 15 Jul 1966, *A.S. Harrison 111.1* (DAO); Ross Lake, Skagit River Valley, near Canada-U.S.A. border, ca. 1000 ft, 12 Jun 1974, *K.I. Beamish, J. Pinder-Moss, C. Selby, J. Pojar & E. Perkins 74040* (DAO, UBC); Mount Warburton-Pike, Saturna Island, 14 Jun 1974, *G. Krause s.n.* (UBC); UBC campus, S of Asian Centre, 29 Jun 1975, *A. Guppy s.n.* (UBC); 1 mi NE of Kaleden, 1800 ft, 23 May 1977, *B. Wikeem & S. Gale s.n.* (UBC); SW coast of Vancouver Island, China Beach, 2 Aug 1980, *H.L. Dickson et al. 3804* (DAO); Harrison Hot Springs, along road which goes along Harrison Lake to Sasquatch Provincial Park, 6 Aug 1980, *H.L. Dickson 3856* (DAO); W end of Manning Provincial Park, Hwy 3 at 2 Mile Creek, 2 km E of Hope, 29 Jun 1982, *S.G. Aiken & S.J. Darbyshire 2081* (DAO); Cowichan District, Salt Spring Island, Mount Taum, above Cape Keppel, 950 ft, 3 Jul 1982, *S.G. Aiken, S.J. Darbyshire & L.E. Pavlick 2140* (DAO); Pacific Rim National Park, Long Beach, Schooner Trail,

4 Jul 1982, *S.G. Aiken & S.J. Darbyshire 2171* (DAO); Pacific Rim National Park, Long Beach Unit, Wickaninnish Beach, Quisitis Point, 5 Jul 1982, *S.G. Aiken & S.J. Darbyshire 2173* (DAO); Vancouver, UBC, along Chancellor Blvd., near University Hill Elementary School, Univ. Endowment Lands, 28 May 1986, *G.B. Straley 3592* (UBC); Galiano Island, W of Stockade Hill, overlooking Montague Harbour, 17 Aug 1986, *W. Crins 7349* (UBC); Meager Creek Hot Springs, N of Pemberton, Lillooet District, 150 m, 1 Jun 1987, *A.A. Rose s.n.* (UBC); Abbotsford, intersection of Hwys. 1 and 11 along ramp, 29 Jun 1988, *S.J. Darbyshire 3729* (DAO); Mount Bruce, summit, 3 Jul 1988, *S.J. Darbyshire & J A. Darybshire 3777* (DAO); 0.25 km E of Vaseux Lake, 1110 m, 13 Jun 1991, *G.W. Douglas 12541* (UBC); Vaseux Lake, S end of Mud Lake, W side, 13 Jun 1991, *T. Goward 91-435* (UBC); Abbotsford Dist. Munic., near base of Sumas Mt, 25 May 1995, *H. Kennedy, F.R. Ganders, M. Marshall, D. Justice & L. Goertzen s.n.* (UBC); Sooke hills, Ragged Mountain ERP, 380 m, 27 Jun 1996, *J.L. Penny & H. Roemer 82* (UBC); along Hwy 33, 33.5 km S of Beaverhill, 25 Jun 2003, *J.M. Saarela & A. Roe 255* (CAN); alongside parking lot at UBC Museum of Anthropology, 25 May 2005, *J.M. Saarela 300* (CAN, UBC); Kuskanook Rest Area, Kuskanook Harbour Society, 24 May 2006, *J.M. Saarela 452* (CAN, UBC); Horseshoe Bay, Whytecliff Park, 27 May 2006, *J.M. Saarela 507* (CAN, UBC); Horseshoe Bay, Eagleridge Drive, just S of Hwy 1 (Trans-Canada Highway), 27 May 2006, *J.M. Saarela 513* (CAN, UBC); Ladner, S side of Canoe Passage, W terminus of River Road, 28 May 2006, *J.M. Saarela & C. J. Sears 537, 538* (CAN, UBC); W of Osoyoos, 1.3 km up Richter Mountain Road, 19 Jun 2006, *J.M. Saarela, C.J. Sears & J. Maze 632* (CAN, UBC); 0.5 km up Grizzly Road, S of Hwy 3, ca. 5 km E of Osoyoos, 20 Jun 2006, *J.M. Saarela, C.J. Sears & J. Maze 646* (CAN, UBC); roadside pullout on W side of Hwy 1 (TransCanada) at Hells Gate, 22 Jun 2006, *J.M. Saarela, C.J. Sears & J. Maze 734* (CAN, UBC); Richmond, London Farm, Gilbert Beach, just E of London's Landing, 28 May 2006, *J.M. Saarela & C. J. Sears 523a* (CAN, UBC); Ladner Harbour Park, 28 May 2006, *J.M. Saarela & C. J. Sears 531* (CAN, UBC); Mayne Island, cliff edge of Mount Parke, ca. 1 km W of highest point where radar tower is, 3 Jun 2007, *J.M. Saarela, D.M. Percy, Y. Chang, & Q.C.E. Cronk 803* (CAN, UBC); Vancouver Island, Island View Park, S of Hwy 17 between Sidney and Victoria, along coast, 4 Jun 2007, *J.M. Saarela, D.M. Percy & Y. Chang 851* (CAN, UBC); Vancouver Island, Thetis Lake Regional Park, just N of Hwy 1, N of Langford, 4 Jun 2007, *J.M. Saarela, D.M. Percy & Y. Chang 859* (CAN, UBC); Vancouver Island, just S of Chemanus along Hwy 1A, 4 Jun 2007, *J.M. Saarela, D.M. Percy & Y. Chang 906* (CAN, UBC); Vancouver Island, just off Hwy 19A along Crane Road, N of Qualicum Beach, at confluence of Nile Creek and the Straight of Georgia, 7 Jun 2007, *J.M. Saarela, D.M. Percy & Y. Chang 934a* (CAN, UBC); Queen Charlotte Islands: Moresby Island, Moresby Camp, Gillett Arm of Cumshewa Inlet, 11 km from Y junction of the loop road, 25 Jul 2007, *J.M. Saarela & D. M. Percy 1271* (CAN, UBC).

6. Bromus inermis Leyss., Fl. Halens. 16. 1761. (**Figs. 5C, 8A–E**). *Festuca inermis* (Leyss.) DC. & Lam., Fl. Franc. 3:49. 1805. *Schedonorus inermis* Beauv., Ess. Agrost. 99:177. 1812. *Forasaccus inermis* (Leyss.) Lunell, Amer. Midl. Naturalist 4:225. 1915. *Zerna inermis* (Leyss.) Lindm., Svensk Fanerogamfl. 101. 1918. *Bromopsis inermis* (Leyss.) Holub, Folia Geobot. Phytotax., Praha 8:167. 1973. Type: EUROPE. Germany: in pratis fertilibus succulentis Pomariis in den Pulverweiden im Amstgarten ad Belberg Crollwitz et alibi frequens, *Leysser s.n.* (holotype: LINN).

Bromus pumpellianus var. *melicoides* Shear, Bull. Div. Agrostol., U.S.D.A. 23:50. 1900. Type: U.S.A. Colorado: Beaver Creek Camp, alt. ca. 3400 m, 8 Jul 1896, *L. H. Pammel s.n.* (holotype: US-81589!). Note: Hitchcock (1935) and Pavlick et al. (2003) included this taxon as a synonym of *B. pumpellianus*, but the holotype clearly is *B. inermis*, based on the absence of awns and scarce lemma pubescence.

Bromus inopinatus Brues, Trans. Wis. Acad. Sci. 17:73. 1911. Type: U.S.A. Wisconsin: Milwaukee, McKinley Park, along shores of Lake Michigan, 21 [no month] 1904, *B.B. Brues 78* (isotype: US-3168443!, fragment).

Bromus inermis f. *proliferus* Louis-Marie, Rev. Oka Agron. Inst. Agric. 14:14. 1940. Type: Canada, Quebec: La Trappe, 24 Aug 1931, *P. Louis-Marie 318* (holotype: QFA).

Bromus inermis f. *bulbiferus* Moore, Rhodora 43:76. 1941. Type: U.S.A. Minnesota: Ramsey County, Cleaveland Ave., 4 mi N of the campus of Minnesota College of Agriculture, 11 Oct 1938, *Kaufman s.n.* (holotype: MINN).

Perennial; strongly rhizomatous; basal leaves decaying into straight fibres, though not readily, plants 21–150 cm tall. Culms 2.9–6 mm wide at base, smooth; nodes 3–4, brown, glabrous or minutely pubescent, hairs to 0.2 mm long. Leaf sheaths closed for most of their length, glabrous or pubescent with soft hairs to 1.2 mm long or stiff hairs to 0.6 mm long; auricles absent or rudimentary; ligules 1.5–3.5 mm long, membranous, glabrous, erose; blades 10–21.5 cm long, 3.8–11.5 mm wide, adaxial surfaces glabrous with occasional long, soft hairs to 1.2 mm long or with dense soft hairs to 0.8 mm long, abaxial surfaces glabrous or pubescent with short hairs to 0.3 mm distributed along blade center, margins serrulate. Panicles 6.5–22 cm long, 3.5–14 cm wide, open; branches erect to ascending, often nodding at maturity, scabrous, usually longer than spikelet, 1–5 spikelets; lowest inflorescence node with 3–7 branches. Spikelets 1.7–3.2 cm long (including awns); florets 7–10. Glumes subequal, lanceolate, glabrous, midnerves scabrous or with hairs to 0.2 mm long; lower glumes 4.1–7 mm long, 1(–3)-nerved; upper glumes 6–9.5 mm long, 3-nerved. Lemmas 10–13.5 mm long, 1.5–2.5 mm wide, glabrous or variously scabrous or puberulent on lower 1/6 to ¼, nerves scabrous; awns absent or to 3 mm long, arising 0–0.5 mm below lemma apex, straight, antrorsely scabrous. Paleas 8–10.5 mm long, shorter than lemmas, keels ciliate throughout, the cilia ca. 0.2 mm long. Stamens 3; anthers 4–5.5 mm long, yellow. $2n = 28, 56$.

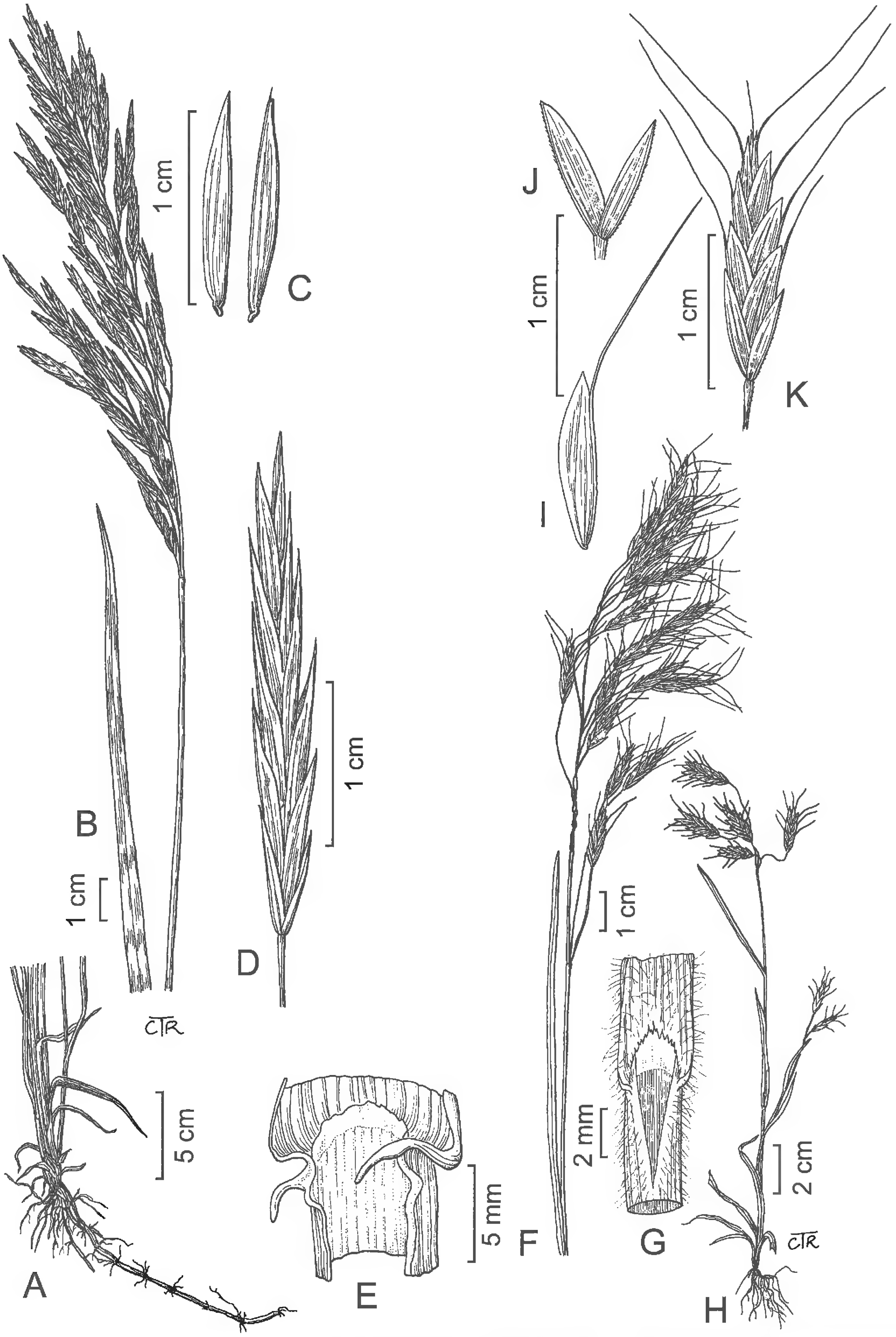

Fig. 8. *Bromus inermis*. A. Rhizome. B. Inflorescence. C. Lemmas. D. Spikelet. E. Ligule. *Bromus japonicus*. F. Inflorescence. G. Ligule. H. Habit. I. Lemma. J. Glumes. K. Spikelet.

Distribution and Habitat.—Introduced. *Bromus inermis* is native across central Eurasia, and introduced in Africa, Australia, North America and South America. It is distributed widely across North America and it is extremely common (Pavlick & Anderton 2007). *Bromus inermis* has been collected throughout British Columbia, mostly on southern Vancouver Island, in the Vancouver area and east of the coastal ranges (Fig. 5C; also see Otfinowski et al. 2007:188). Habitats include roadsides, fields and pastures, wet meadows and open woods. Elevation: 0–1256 m.

Common Names.—English: Austrian brome, Austrian brome grass, awnless brome, awnless brome grass, Hungarian brome, Hungarian brome grass, Hungarian fodder grass, Russian brome, smooth brome, smooth brome grass; French: brome inerme, brome de Hongrie, brome sans arêtes.

Notes.—The introduced *B. inermis* and the native *B. pumpellianus* have been variously treated as the same (e.g., Elliott 1949; Wagnon 1952; Scoggan 1978) or separate species (e.g., Pavlick 1995; Pavlick & Anderton 2007). Elliott (1949) demonstrated that the taxa are partially interfertile and presented morphological evidence (i.e., intermediate specimens) indicating that hybridization has likely occurred between the taxa. Nevertheless, the taxa have different morphological characteristics and native distributions and they occur in different habitats, suggesting that they have independent evolutionary histories. *Bromus inermis* is also morphologically similar to the relatively recently introduced *B. riparius* (see discussion under that taxon).

Bromus inermis was introduced into North America in 1884 by the California Agricultural Experimental Station. In Canada it is widely cultivated for hay and pasture and used in revegetation projects, but although economically beneficial as forage, *B. inermis* is extremely invasive and poses serious threats to Canadian ecosystems (Otfinowski et al. 2007). It was recently ranked as the 8th most serious invasive alien plant threatening natural habitats in Canada (Catling & Mitrow 2005). Otfinowski et al. (2007) provide a detailed review of the biology of *Bromus inermis*.

Representative Specimens Examined. **CANADA. British Columbia:** Bridge Creek, 21 Sep 1896, *W. Allan s.n.* (UBC); Goldstream, Okanagan, 11 Jul 1904, *J.R. Anderson s.n.* (UBC); Kamloops Lake, 4 Jul 1906, *E. Wilson 678* (UBC); Coombe, Surrey, 27 Jun 1910, *C. E. Britton s.n.* (UBC); E of Field, 1-2 Aug 1914, *A.S. Hitchcock 11543* (US); Big Creek, Jun 1915, *M. Bertrand s.n.* (UBC); Vernon, 20 June 1917, *E.M. Warren s.n.* (UBC); Quesnel Dam, 1 Nov 1917, *W. Newcombe 317* (UBC); Merritt, 28 Aug 1920, *G.W. Copley 10-9* (UBC); Castlegar, 3 Jul 1937, *J.W. Eastham s.n.* (UBC); Procter, Nelson, 7 Jul 1937, *J.W. Eastham s.n.* (UBC); Ymir Rd, Nelson, 10 Jul 1937, *J.W. Eastham s.n.* (UBC); Mirror Lake, Kaslo, 12 Jul 1937, *J.W. Eastham s.n.* (UBC); Marble Mts, Hat Creek Valley, 26 Jun 1938, *J.W. Thompson & E.M. Thompson 228* (CAN); Kamloops, Dominion Experimental Station, 12 Jun 1940, *J.W. Eastham s.n.* (UBC); Manning Park, Hope-Princeton, 9 Aug 1945, *G.A. Hardy s.n.* (UBC); Cache Creek, 29 Jul 1946, *J. A. Rattenbury s.n.* (UBC); Prince George, 20 Jul 1955, *S. Lenaelou 16* (UBC); 2nd Trapp Lake, Kamloops, 19 Aug 1950, *V.J. Krajina s.n.* (UBC); Kamloops District, Trap Lake, 27 Aug 1950, *V.J. Krajina s.n.* (UBC); Edgewood, Arrow Lake, 1500 ft, 9 Jun 1957, *K. Beamish & A. Gilmartin 7288* (UBC); Keene Creek, Kaslo, Kootenay, 16 Jul 1960, *M. Bell s.n.* (UBC); Tranquille, 6 Oct 1962, *V.C. Brink s.n.* (UBC); Mt Seymour summit, Aug 1963, *H. H. Ross s.n.* (UBC); Chilcotin, plot no. 110, Aug 1968, *C. Beil 68-8-14* (UBC); Fort Nelson near Mile 300 of the Alaska Highway, 3 Jul 1970, *R.M. Annas, V.J. Krajina & R.G. McMinn s.n.* (UBC); Maxhamish Lake, 7 Jul 1970, *R.M. Annas, V.J. Krajina & R.G. McMinn s.n.* (UBC); Cariboo Parklands, near confluence of Chilcotin and Fraser Rivers, 20 Jun 1972, *J.F. Hyne 156* (UBC); Lakit Mountain lookout, 18 Aug 1974, *F. Fodor 940* (UBC); Callanan Lake, Chilcotin, 8 Jul 1975, *D. Jenkins 10122* (UBC); 3 mi W of Red Pass Park Headquarters, 17 Jul 1975, *C.C. Chuang 75/5* (UBC); Sundance Lake, Peace River District, 2200 ft, 3 Jul 1978, *A.A. Rose AAR 78* (UBC); Brunswick Pt. delta, 6 Jun 1979, *G.E. Bradfield 91* (UBC); Ray Farm, 11 km S of Clearwater Lake, Wells Gray Park, 21 Jun 1979, *T. Goward 81-326* (UBC); along Rt. 12, ca. 47 km W of jct with Rt. 97, N of Cache Creek, 21 Jun 1983, *G.B. Straley 2691* (UBC); New Westminster, 18 May 1989, *F. Lomer 89-015* (UBC); Osoyoos area, just NE of Chapaka border crossing, W bank Similkameen River near border (Indian Reserve), 2 Jun 1990, *T. Goward 90-804* (UBC); along road to Tumbler Ridge, a few km S of junction with Rt. 97 at Arras, near Dawson Creek, 27 Jul 1991, *G.B. Straley & K.W. Nicholls 6866* (UBC); Spatsizi, Cold Fish Lake, 16 Aug 1992, *V.C. Brink s.n.* (UBC); Kootenay, Grand Forks, Gilpin Forest Service Road, E of Grand Forks, 23 Jun 1993, *L.E. Pavlick 93-141* (UBC); Kootenay, Windermere Creek, adjacent to creek at Boy Scout Camp "Woodsmoke", 27 Aug 1998, *H. Stewart 98091808* (UBC); 18 mi N of Dease Lake (Brady Creek) on Hwy 37 towards Watson Lake, 20 Jul 2004, *P.M. Peterson, J.M. Saarela & S. Smith 18668* (CAN, US); 1 mi S of Iskut on Hwy 37 towards Meziadin Junction, along Coyote Creek, 20 Jul 2004, *P.M. Peterson, J.M. Saarela & S. Smith 18673* (CAN, US); 18 mi N of Dease Lake (Brady Creek) on Hwy 37 towards Watson Lake, 20 Jul 2004, *P.M. Peterson, J.M. Saarela & S. Smith 18668* (CAN, US); 1 mi S of Iskut on Hwy 37 towards Meziadin Junction, along Coyote Creek, 20 Jul 2004, *P.M. Peterson, J.M. Saarela & S. Smith 18673* (CAN, US); along Hwy 3 at Kettle River, vacant lot beside river across from "Gold Pan Café and Store", 18 May 2006, *J.M. Saarela 345* (CAN, UBC); Fort Steele Road, corner of Hwy 3 and Wardner, 12 km W of Jaffray, 23 May 2006, *J.M. Saarela 412* (CAN, UBC); ca. 2 km E of Erickson along Hwy 3, 24 May 2006, *J.M. Saarela 439* (CAN, UBC); Osoyoos, Haynes Provincial Park, 25 May 2006, *J.M. Saarela 481, 485* (CAN, UBC); Ladner, S side of Canoe Passage, W terminus of River Road, 28 May 2006, *J.M. Saarela & C. J. Sears 540* (CAN, UBC); Manning Provincial Park, 0.9 km up road across from park lodge that goes to alpine area, 19 Jun

2006, *J.M. Saarela, C.J. Sears & J. Maze 566* (CAN); Princeton, across from Princeton High School, 19 Jun 2006, *J.M. Saarela, C.J. Sears & J. Maze 597* (CAN, UBC); along Finmore Road, W of Prince George, S of Stuart River Provincial Park, along small road S of road to Cobb Lake and N of Beverly Lake Forest Service Road, 18 Jul 2007, *J.M. Saarela & D. M. Percy 1033* (CAN, UBC); old gravel mining area, just S of Hwy 16, N of Bulkley River, just E of Ross Lake, 19 Jul 2007, *J.M. Saarela & D.M. Percy 1088* (CAN, UBC); S of 100 Mile House, down 83 Mile Road to Green Lake Prov. Park, 28 Jul 2007, *D.M. Percy 1366* (CAN, UBC).

7. Bromus japonicus Thunb. in Murray, Syst. Veg., ed. 14. 119. 1784. Thunb. Fl. Jap. 52. 1784, serius. **(Figs. 8F–K, 9A)**. *Bromus arvensis* var. *japonicus*, Nuov. Fl. Italia 1:149. 1923. *Serrafalcus japonicus* (Thunb.) Willmott., Man. Brit. Bot. (Babington), ed. 10. 510. 1922. Type: JAPAN: *Thunberg s.n.* (holotype: UPS).

Annual; rhizomes absent; plants 17–85 cm tall. Culms 1–2.2 mm wide at base, smooth; nodes 3–4, black-brown. Leaf sheaths closed for most of their length, densely pilose with soft, wavy hairs to 1.2 mm long; auricles absent; ligules 1–2.2 mm long, membranous, glabrous, apex erose; blades 3.5–13 cm long, 1–6 mm wide, adaxial and abaxial surfaces densely pubescent with short, stiff hairs to 0.6 mm long, margins smooth or serrulate. Panicles 3–26 cm long, 6–16 cm wide, open; branches spreading to ascending (lower branches sometimes nodding), flexuous, smooth to scabrous, usually longer than spikelets, 1–6 spikelets per branch, lowest inflorescence node with 1–6 branches. Spikelets 1.8–4.2 cm long, broadly oblong to ovate-lanceolate, terete to moderately compressed, rachillas sometimes visible at maturity, florets 7–15. Glumes subequal, smooth, margins sometimes hyaline; lower glumes 4–7 mm long, 3–5(–7)-nerved; upper glumes 5–8 mm long, 7–9-nerved. Lemmas 7–9.2 mm long, 1.2–2.2 mm wide, 7–9-nerved, nerves not conspicuous, backs glabrous or scabridulous, scabrules ca. 0.1 mm long, hyaline margins 0–0.5 mm wide at widest point, apex minutely bifid, the cleft to 1 mm deep; awns 4.2–13 mm long (awn on lowest lemma usually shorter), arising 1.5–2.6 mm below lemma apex, straight to strongly divergent, widest at base, antrorsely scabrous. Paleas 6–7 mm long, backs glabrous, keels ciliate, cilia 0.3–0.5 mm long. Anthers 2; stamens 0.6–1.1 mm long, brown. $2n = 14$.

Distribution and Habitat.—Introduced. *Bromus japonicus* is native to Europe. In North America, *B. japonicus* is distributed widely throughout the U.S.A. and in southern Canada (Pavlick & Anderton 2007). *Bromus japonicus* has been collected in various places throughout British Columbia; it is most common in the interior of the province (Fig. 9A). Habitats include roadsides, grassy areas, hillsides and meadows. Elevation: 152–1050 m. Whisenant (1990) suggested that *B. japonicus* has become problematic in areas that have reduced occurrence of fire and grazing by large animals.

Common Names.—English: Japanese chess, Japanese bromegrass, Japanese brome, spreading brome; French: brome du Japon, brome japonais.

Notes.—The authority for this name has been variously attributed to 'Thunberg', 'Thunberg ex Murray', 'Thunberg in Murray', and 'Murray', because it was published in both *Flora Japonica* (Thunberg, 1784, August) and *Systema Vegetabilum*, ed. 14 (Murray 1784, May-June), being attributed to Thunberg in the latter. Because of this confusion, Bartholomew et al. (Taxon 46:311-314. 1997) considered the author citations of the many new names published in these works and concluded that their authorship should be attributed to 'Thunberg in Murray' when a complete bibliographic citation is given (as above), or as 'Thunberg' when only the authority is provided.

Bromus japonicus and *B. squarrosus* are morphologically similar species, distinguished on the basis of their hyaline lemma margin widths and their degree of panicle branching (see Taxonomic Key). Some individuals with seemingly intermediate morphologies can be difficult to determine, but the taxa have consistently been recognized as distinct species in their native and introduced ranges. Molecular (Ainouche & Bayer 1997; Ainouche et al. 1999) and serological data (Smith 1972) indicate that they are closely related. Based on allozyme and morphometric data, Oja et al. (2003) suggested that the two taxa might be more appropriately recognized as intraspecific taxa of a single polymorphic species. Oja et al. (2003) did not, however, propose a formal taxonomic revision of the group. I recognize these taxa here at the species level.

Representative Specimens Examined. **CANADA. British Columbia:** Armstrong, 31 May 1928, *J.B. Munro s.n.* (V); near Kamloops, 2000 ft, 27 May 1934, *G.V. Copley 7* (US); Kamloops, Mission Flats, 1200 ft, 22 Jun 1937, *E.W. Tisdale 40-10* (US); Tranquille Ranges, Tranquille, 21 Jul 1939, *H. Groh 244* (DAO); 2 mi NW of Roosville, on overgrazed Indian Reserve, Jul 1947, *H.K. DeBeck s.n.* (DAO, UBC, V); Goose Lake

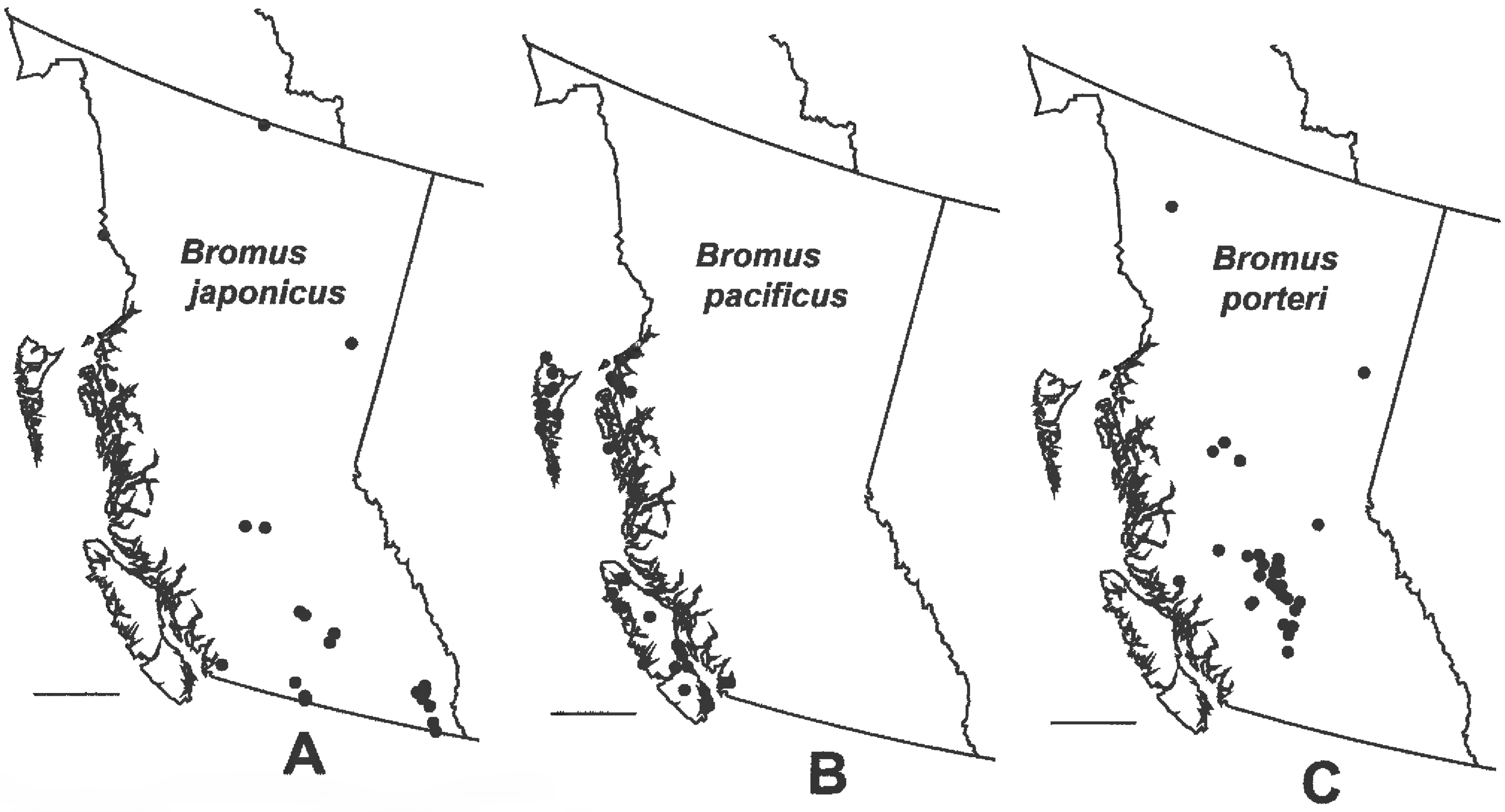

Fig. 9. Geographic distribution in British Columbia. A. *Bromus japonicus*. B. *Bromus pacificus*. C. *Bromus porteri*. Scale bars = 200 km.

about 3 mi N of Vernon, 6 Jul 1953, *J.A Calder & D.B.O. Savile 10145A* (DAO); 4.5 mi WSW of Kamloops, 2300 ft, 10 Jul 1953, *J.A.Calder & D.B.O. Savile 10297* (DAO, US); two mi W of Kamloops, 26 Jul 1955, *G.A. Mulligan & W. Woodbury 1817* (DAO); Stikine River, between Taya and Tahltan Rivers, 500 ft, 10 Sep 1977, *A.A. Rose 77-778* (UBC); Lake Koocanusa, Kikomun Creek Provincial Campground, 15 Jul 1993, *F. Lomer 93-117* (UBC); 7.6 km W of Osoyoos along Hwy 3, 25 May 2006, *J.M. Saarela 487* (CAN, UBC); 5.6 km S of Hwy 3 on Mount Kreger Road, South Okanagan Grasslands Protected Area, 20 Jun 2006, *J.M. Saarela, C.J. Sears & J. Maze 673* (CAN, UBC).

8. Bromus pacificus Shear, Bull. Div. Agrostol., U.S.D.A. 23:38, f. 21. 1900. (**Figs. 9B, 10A–E**). *Bromopsis pacifica* (Shear) Holub, Folia Geobot. Phytotax. 8:168. 1973. Type: U.S.A. Oregon. Clatsop Co.: in moist thickets near the seashore, S of Seaside, 11 Aug 1899, *C.L. Shear & F.L. Scribner 1703* (holotype: US-1867129!; isotype: US-81585!).

Bromus magnificus Elmer, Bot. Gaz. 36:53. 1903. Type: U.S.A. Washington. Clallam Co.: Aug 1900, *A.D.E. Elmer 1957* (holotype: DS; isotype: US-401765!, with additional locality information: "Olympic Mtns.").

Perennial; rhizomes absent; plants 45–172 cm tall. Culms 4–5 mm wide at base, smooth; nodes 5–9, brown, finely to densely retrorsely pubescent, hairs to 0.7(–1) mm long, occasionally glabrous with hairs above and below nodes. Leaf sheaths closed for most of their length, open for 14–35 mm in length, glabrous or sparsely to densely pilose with hairs to 2.1 mm long; auricles absent; ligules 2–4 mm long, membranous, glabrous, erose; blades to 32(–37) cm long, 7–16 mm wide, adaxial surface pilose, hairs to 1.5 mm long, soft and wavy, abaxial surface glabrous, margins smooth or serrulate. Panicles 17–28 cm long, 12.5–19 cm wide, open; branches mostly spreading and/or nodding, scabrous to pubescent, longer than spikelets, 1–6 spikelets per branch; lowest inflorescence node with 1–4 branches. Spikelets 2.1–3.8 cm long, ovate-lanceolate, terete to slightly compressed, rachillas sometimes visible at maturity, particularly distally; florets (4)6–8(10). Glumes slightly subequal, pubescent, hairs to 0.6 mm long, longer hairs sometimes restricted to keel; lower glumes 8.2–10.5 mm long, 1-nerved, lanceolate; upper glumes 9.7–12 mm long, 3-nerved, lanceolate to strongly acuminate with mucros 0–1.3 mm long. Lemmas 10–13.5 mm long, 1.8–2.3 mm wide, 7-nerved, sparsely to densely pubescent with appressed hairs to 1.5 mm long, longest hairs sometimes along margins, hairs sometimes denser on lower ½, apex entire or minutely bifid, the cleft 0–0.3 mm deep; awns 3–6.5(–7) mm long, arising 0–0.1 mm below lemma apex, straight, antrorsely scabrous. Paleas 9–10.5 mm long, usually shorter than lemmas, keels densely ciliate, cilia to 0.5 mm long. Stamens 3; anthers 2–3 mm long, dark brown. $2n = 28$.

Distribution and Habitat.—Native. *Bromus pacificus* occurs along or near the Pacific coast from south-

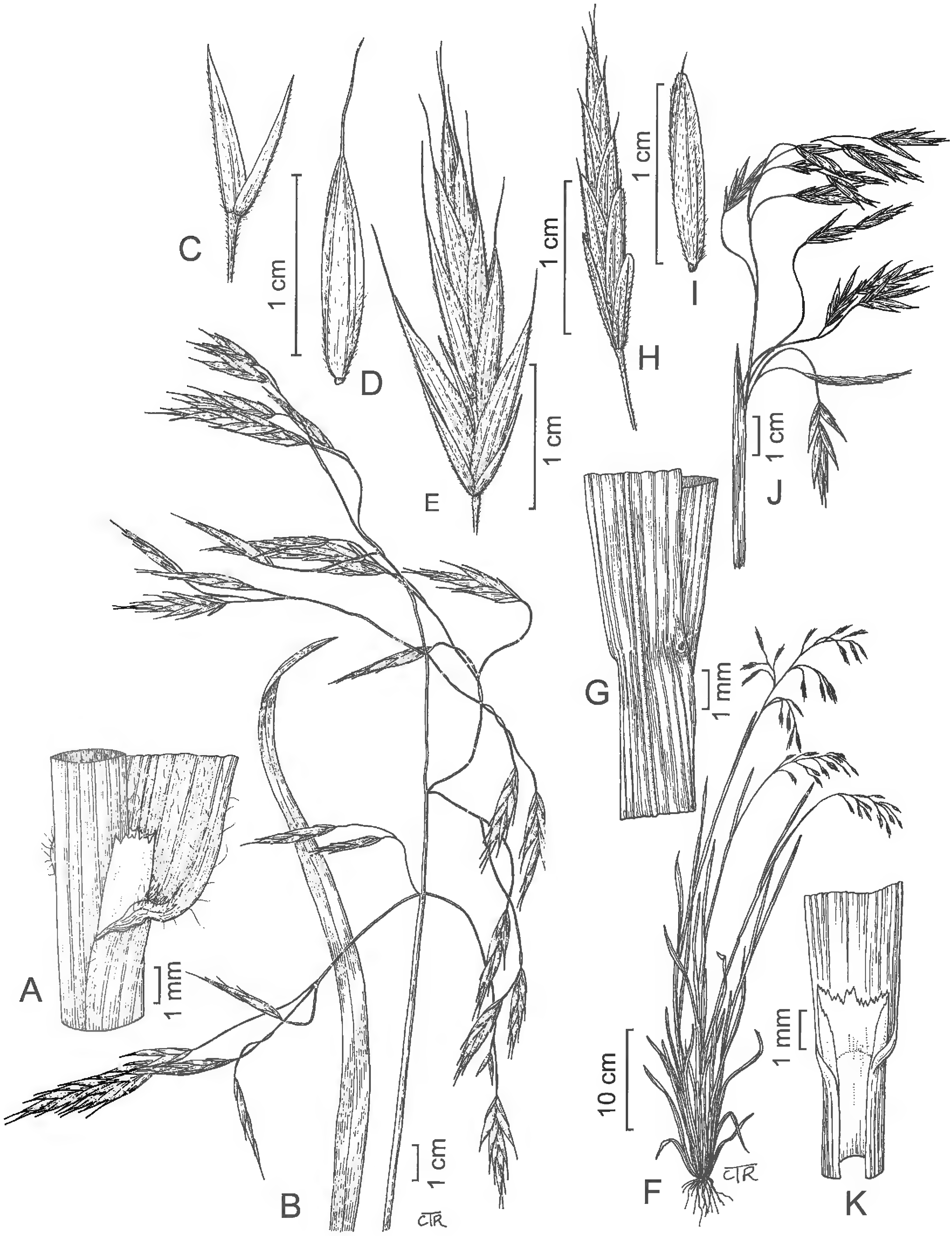

FIG. 10. *Bromus pacificus*. A. Ligule. B. Inflorescence. C. Glumes. D. Lemma. E. Spikelet. *Bromus porteri*. F. Habit. G. Collar. H. Spikelet. I. Lemma. J. Inflorescence. K. Ligule.

eastern Alaska to central Oregon (Pavlick & Anderton 2007). Pavlick & Anderton (2007) indicated that *B. pacificus* also occurs in northern California, based on two specimens from HSC identified as *B. pacificus* (M. Barkworth, pers. comm.). Examination of these specimens indicates that they were incorrectly determined [*Barker 1035* (HSC-44691!) from Del Norte Co. is *B. vulgaris*; and *Anderson 5120* (HSC-22840!) from Humboldt Co. is *B. carinatus* Hook. & Arn. var. *marginatus* (Nees) Barkworth & Anderton]. *Bromus pacificus* is not known from California (Saarela & Peterson, in press). In British Columbia, *B. pacificus* occurs in coastal regions of the province (Fig. 9B); absence of collections along much of the coastline likely reflects a paucity of collecting activities in difficult-to-access areas, rather than the absence of the species. Habitats include moist ravines, shaded woods, grassy swards, saline beaches, ditches and along roadsides. Elevation: 0–50 m.

Common Names.—Pacific brome, Shear Pacific brome.

Notes.—Many *B. pacificus* specimens from British Columbia have previously been determined incorrectly as species of *B.* sect. *Ceratochloa* (i.e., *B. carinatus* or *B. sitchensis*). With large, open panicles, *B. pacificus* is superficially similar to these taxa, but it can be easily distinguished from them by its lemmas that are rounded or slightly keeled over the back (vs. lemmas that are strongly laterally flattened and keeled in species of *B.* sect. *Ceratochloa*), and 1- and 3-nerved lower and upper glumes (vs. 3–5- and 5–9-nerved lower and upper glumes, respectively). Additionally, *B. pacificus* occurs only on or near the coast, whereas plants in *B.* sect. *Ceratochloa* are distributed much more widely.

Representative Specimens Examined. **CANADA. British Columbia:** Qualicum, Vancouver Island, 29 Jul 1887, *Macoun 30008* (CAN, US); Renfrew, 18 Jul 1902, *C.O. Rosendahl 776* (CAN, US); Sidney, Vancouver Island, 30 May 1914, *M.O. Malte s.n.*(DAO); Courtenay River, Comox, 10 Jul 1915, *J. Macoun s.n.* (V); Courtenay, 23 Jul 1915, *M.O. Malte 108338* (CAN, DAO); Alberni, Jul 1916, *W. R. Carter s.n.* (V); Prince Rupert, 1 Aug 1916, *M.O. Malte 106910* (CAN, DAO); Vancouver Island, Port Alberni, head of Alberni Canal, 18 Aug 1922, *J. Davidson s.n.* (UBC); Triangle Island, 28 Jun 1949, *G. Hardy 21645* (V); Queen Charlotte Islands, Moresby Island, Louscoone Inlet, 13 Sep 1951, *R. Pillsbury s.n.* (UBC); shore of Duncan Bay ca. 6 mi WNW of Prince Rupert, 24 Aug 1954, *J.A. Calder, D.B.O. Savile & J.M. Ferguson 14973* (DAO); Indian Village near Henslung Bay, Langara Island off NW tip of Graham Island, 16 Jul 1957, *J.A. Calder, D.B.O. Savile & R.L. Taylor22539* (DAO); near Juskatla on Juskatla Inlet, Graham Island, 8 Aug 1957, *D.B.O. Savile 3520* (DAO); Yakoun River Delta S of Port Clements, Masset Inlet, Graham Island, 15 Aug 1957, *J.A. Calder & R.L. Taylor 23507* (DAO); Queen Charlotte Islands, Deena River mouth, E entrance to Skidegate Channel, 27 Aug 1957, *J.A. Calder & R.L. Taylor 23789* (DAO, UBC); Markale, Kyuquot, 1 Jul 1958, *Taylor 143* (UBC); Kyuquot, Mckay cove, 8 Jul 1958, *Taylor 383* (UBC); Queen Charlotte Islands: Moresby Island, W end of S arm of Kootenay Inlet, 22 Jul 1964, *J.A. Calder & R.L. Taylor 36201* (DAO, UBC); Kaisum ancient Haida village, Moresby Island, 4 Aug 1964, *J.A. Calder & R.L. Taylor 36523* (DAO); Tee Island, E side of Naden Harbour, Graham Island, 12 Aug 1964, *J.A. Calder & R.L. Taylor 36848* (DAO); Long Island, Vancouver Island, 19 Aug 1965, *Taylor 6740* (UBC); W of Truck Narrows, Truck Inlet, ca. 7 mi N of Prince Rupert, range 5, Coast District, 31 Jul 1973, *V. Krajina s.n.* (UBC); Vancouver Island, Tofino, Meares Island, lake and creek S of Lone Creek, 1 Jul 1981, *A. Ceska, O. Oldriska, & R.T. Ogilvie s.n.* (UBC); Vancouver Island, Nitinat Camp, junction of Nitinat Camp Road & Cowichan, Nitinat Lake Road, 21 Aug 1989, *L.E. Pavlick 89-158* (UBC); Vancouver Island, Port Alberni, near mouth of Somass River, 11 Sep 1993, *J. Cayouette C7592* (DAO); Port Moody, Rocky Point Park at head of Burrard Inlet, about 14 km E of Vancouver, 5 August 1996, *F. Lomer 96-128* (UBC); Queen Charlotte Islands, Moresby Island, 11 km SE of Sandspit, Sheldens Lagoon, 0 m, 18 Jul 1997, *F. Lomer & N. Grove 97407* (V); mouth by Mission Creek, W edge of Kincolith (Ginglox), 22 Jul 2004, *P.M. Peterson, J.M. Saarela & S. Smith 18719* (CAN, US); entrance to Ferry at Prince Rupert, 23 Jul 2004, *P.M. Peterson, J.M. Saarela & S. Smith 18729* (CAN, US); Vancouver Island, Rupert Inlet, 4 Sep 2006, *J.M. Saarela 760* (CAN, UBC); Queen Charlotte Islands: Graham Island, Rennell Sound Recreation Site, at end of Rennell Sound Forest Service Road at Rennell Sound, ca. 36 km NW of Queen Charlotte City, 23 Jul 2007, *J.M. Saarela & D.M. Percy 1202* (CAN, UBC); Rainbow Pass, Coast Mountains, along Hwy 16, E of Prince Rupert, 26 Jul 2007, *J.M. Saarela & D.M. Percy 1308* (CAN, UBC); along Hwy 16, adjacent to Skeena River between Tyhee and Skeena, 26 Jul 2007, *J.M. Saarela & D.M. Percy 1311* (CAN, UBC).

9. Bromus porteri (J.M. Coult.) Nash, Bull. Torrey Bot. Club 22:512. 1895. (**Figs. 9C, 10F–K**). *Bromus kalmii* var. *porteri* J. M. Coult., Man. Bot. Rocky Mt. 425. 1885. *Bromus ciliatus* var. *porteri* (J. M. Coult.) Rydb., Contr. U.S. Natl. Herb. 3:192. 1895. *Bromopsis porteri* (J. M. Coult.) Holub, Folia Geobot. Phytotax. 8:168. 1973. Type: U.S.A. Colorado. Lake Co.: Twin Lakes, 25 Jul 1872, *T.C. Porter s.n* (lectotype: NY, designated by Wagnon, Brittonia 7:471. 1952).

Bromus ciliatus var. *montanus* Vasey ex Beal, Grass. N. Amer. 2:619. 1896. Type: U.S.A. Colorado: 1892, *H.N. Patterson 264* (lectotype: MSC, designated by Beal, Grass. N. Amer. 2:619. 1896; isolectotype: US–1008608!).

Bromus ciliatus var. *scariosus* Scribn., Bull. Div. Agrostol., U.S.D.A. 13:46. 1898. Type: U.S.A. Wyoming. Albany Co.: Sheep Mountain, 3 Jul 1897, *A. Nelson 3305* (holotype: US–1008288!).

Bromus kalmii var. *occidentalis* Vasey ex Beal, Grass. N. Amer. 2:624. 1896. Type: U.S.A. Montana: *Anderson 11* (lectotype: MSC-0091326!, designated here; isotype: US-865498!, fragment and photostat ex. MSC).

Notes: In the protologue for *B. kalmii* var. *occidentalis*, Beal (1896:624) lists three syntypes: (1) Montana, 1883, *W.M. Canby & F.L. Scribner 384*; (2) Montana, *Anderson 11*; (3) Colorado, *Cassidy s.n.* There is a sheet in US (US-1008517; digital photograph!) labeled "*B. ciliatus* or *B. kalmii* var. *occidentalis*" with the following collection information: *F.L. Scribner*, 1883, Northern Pacific R. R. [rail road]. The specimen is annotated in A.S. Hitchcock's hand "Probably Vasey's type of *Bromus kalmii occidentalis* Vasey; Beal's type probably in Herb. Mich. Agr. Coll." The specimen also bears the handwritten annotation "Montana probably." Hitchcock (1935:811) indicated that *Canby & Scribner 384* is the type. The Botanical Type Specimen Registry at the US National Herbarium identifies this as the *Canby & Scribner 384* specimen (http://ravenel.si.edu/botany/types, accessed 12 Jun 2007), but neither Canby's name, the collection number (384), nor the geographic provenance of the specimen (Montana) are indicated on the specimen; it is therefore not absolutely clear that this is the specimen cited in the protologue. Pavlick et al. (2003:172) erroneously indicated that the Canby and Scribner specimen is housed at both MSC and US; there are no sheets of this collection in MSC (*fide* L.A. Prather, 2007). The last two syntypes have been located at MSC (MSC-0091326! and MSC-0091327!), and there is a fragment and a photograph of the Anderson sheet at US (fragm. US-865498; digital photo!) that bears the annotation "*Anderson 11* ex MSC". Pavlick et al. (2003:172) erroneously indicate that this fragment and photograph are the Canby & Scribner collection. In accordance with Article 9.18 of the ICBN (Vienna Code), Hitchcock's choice of type is in conflict with the protologue, and there are other elements available that are are not in conflict with the protologue. Among the Anderson and Cassidy collections, the Anderson collection is most complete. It is most appropriate to designate the Anderson collection as the lectotype because it is a robust specimen and it is not in conflict with the protologue.

Perennial; rhizomes absent; plants 32–100 cm tall. Culms 0.7–1.8 mm wide at base, smooth, sometimes pubescent below inflorescence; nodes 3–8, brown, glabrous, sometimes with minute hairs below nodes; lower nodes covered by sheaths. Leaf sheaths closed for most of their length, glabrous; auricles absent; ligules 0.5–1.9 mm long, membranous, glabrous, erose; blades 7–28 cm long, 1.9–5 mm wide, adaxial surface glabrous, abaxial surface glabrous or with sparse, soft hairs to 1.5 mm, margins smooth or serrulate. Panicles 5–12 cm long, 1.5–7 cm wide, open; branches ascending to drooping, shorter or longer than spikelet, pubescent, 1–2 spikelets per branch, lowest inflorescence node with 1–2 branches. Spikelets 1.7–3.1 cm long, ovate-lanceolate, terete to slightly compressed, rachillas sometimes visible at maturity, particularly distally; florets 4–9. Glumes lanceolate, pubescent, hairs 0.2–0.3 mm long; lower glumes 5.2–7.5 mm long, (1–)3-nerved; upper glumes 6.2–9.5 mm long, 3-nerved. Lemmas 8–10 mm long, 1.5–2.5 mm wide, 7-nerved, densely pubescent with hairs 0.2–1.5 mm long, hairs sometimes denser on lower ½, apex entire or minutely bifid, the cleft 0–0.2 mm deep; awns 0.8–3.1 mm long, arising 0–0.3 mm below lemma apex, straight, antrorsely scabrous. Paleas 7–8.2 mm long, shorter than lemmas, keels ciliate, cilia to 0.3 mm long. Stamens 3; anthers 1.9–2.5 mm long, dark brown. $2n = 14$.

Distribution and Habitat.—Native. *Bromus porteri* occurs in southern Alberta, Saskatchewan and Manitoba and south to western Texas and California (Pavlick & Anderton 2007). In British Columbia *B. porteri* occurs mostly in the interior of the province. Habitat includes dry talus slopes, meadows, open ground, woodland flats and grasslands. Elevation: 152–1310 m.

Common Name. — nodding brome.

Notes.—*Bromus porteri* has been variously treated as a distinct species (e.g., Gould & Moran 1981; Pavlick 1995; Pavlick & Anderton 2007; Scoggan 1978; Soderstrom & Beaman 1968) or as a synonym of *Bromus anomalus* Rupr. ex E. Fourn. (e.g., Douglas et al. 2001; Wilken & Painter 1993). *Bromus anomalus* and *B. porteri* are morphologically and geographically distinct taxa. *Bromus anomalus* is easily separated from *B. porteri* by its 1-nerved lower glumes [vs. (1)3-nerved in *B. porteri*] and conspicuously narrowed midvein of the leaf below the collar (Wagnon 1952; Pavlick 1995; Pavlick & Anderton 2007; J. M. Saarela, personal observation). The two species are largely allopatric. *Bromus porteri* has a wide distribution in western North America where it is distributed from Manitoba to British Columbia and south to California, New Mexico and northeastern Mexico (Wagnon 1952; Pavlick 1995; Herrera Arrieta 2001; Pavlick & Anderton 2007; Saarela & Peterson in press), whereas *B. anomalus* is distributed in Texas and throughout northern and central Mexico (Soderstrom & Beaman 1968; Pavlick et al. 2003; Herrera Arrieta 2001; J. M. Saarela, personal observation). Plants in British Columbia are clearly referable to *Bromus porteri*.

Representative Specimens Examined. **CANADA. British Columbia:** Klinaklini Valley, 3000 ft, 17 Sep 1920, *T. MacKenzie 3-1* (UBC); junction of Banbricker and Big Creeks, Chilcotin, 16 Jul 1929, *J. Davidson 63* (UBC); Chilcotin (E), Riske Creek, 13 Aug 1938, *E.W. Tisdale 40-1* (US); Hanceville, Chilcotin, 24 Jul 1944, *J.W. Eastham 12236* (CAN, UBC); Francois Lake, 6 Jul 1944, *J.W. Eastham s.n.* (UBC); Canoe Creek, Gang Ranch road, 13 Jul 1945, *J.W. Eastham s.n.* (DAO, UBC); above Pavilion Lake, 30 Jul 1946, *V.C. Brink s.n.* (UBC); Old

Forestry Lookout, Ootsa Lake, 8 Jul 1944, *J.W. Eastham s.n.* (UBC); Hanceville, Chilcotin, 24 Jul 1944, *J.W. Eastham s.n.* (V); Cariboo zone, 1 mi S of Farwell Creek, 20 Jul 1967, *C. Beil 67-07-20* (UBC); Chilcotin, plot no. 105, 3500 ft, Aug 1968, *C. Beil 68-8-21* (UBC); Farwell Creek, 19 Jul 1972, *C.E. Beil 282* (UBC); W side of Relay Creek Basin trail ca. 1.5 mi from Relay Creek cabin, 27 Jul 1977, *C. Selby plot 78 #627* (UBC); Relay Creek Basin, 12 Aug 1977, *C. Selby s.n.* (UBC); Stikine River (Ranch), 500 ft, 9 Sep 1977, *A.A. Rose 77-771* (UBC); 0.3 km N of Burn Creek, 0.5 km from Stikine River, 744-824 m, 31 Jul 1979, *W. Gorman 1349* (UBC); 10 km W of Tatla Lake Village, 5 Jul 1980, *L.E. Pavlick 80-14* (V); Cariboo District, Riske Creek, E pasture of Bald Mountain, 12 Jul 1982, *S.G. Aiken, S.J. Darbyshiren & A. Roberts 2287* (DAO); Cariboo District, Alexis Creek, 1 km N of settlement, 17 Jul 1982, *S.G. Aiken & S.J. Darbyshire 2369* (DAO); Thompson-Okanagan, Cornwall Hills, along Cornwall Hills Road, 13 Sep 1989, *L.E. Pavlick 89-212* (UBC, V); Thompson-Okanagan, Hat Creek, along Hat Creek Road, 14 Sep 1989, *L.E. Pavlick 89-263* (UBC); Chasm, 26 Jul 1989, *F. Lomer 89-14* (UBC); Cariboo area, NW of Clinton, White Lake, 13 Sep 1993, *J. Cayouette C7601* (DAO); Cariboo-Chilcotin, Dog Creek area, 7 Jul 1994, *T. Goward & C. Clement 94-513* (UBC); Cariboo-Chilcotin, Dog Creek area, 21 Jul 1994, *T. Goward & C. Clement 94-594* (UBC); Peace River Land District, W of Fort St. John, close to road 29, 10 Sep 1998, *J. Cayouette 8491* (DAO).

10. Bromus pumpellianus Scribn., Bull. Torrey Bot. Club 15:9. 1888. (**Figs. 11A–E, 12A**). *Forasaccus pumpellianus* (Scribn.) Lunell, Amer. Midl. Naturalist 4:225. 1915. *Bromus inermis* subsp. *pumpellianus* (Scribn.) Wagnon, Rhodora 52:211. 1950. *Zerna pumpelliana* (Scribn.) Tzvelev, Fl. Arct. U.R.S.S. 2:225. 1964. *Bromopsis pumpelliana* (Scribn.) Holub, Folia Geobot. Phytotax. 8:168. 1973. Type: U.S.A. Montana. Meagher Co.: Belt Mountains, Meagher County, Montana, 1883, *F. Lamson-Scribner 418* (holotype: US-81590!).

Bromus purgans var. *purpurascens* Hook., Fl.-Bor. Amer. 2:252. 1840. *Bromus inermis* subsp. *pumpellianus* var. *purpurascens* (Hook.) Wagnon, Rhodora 52:211. 1950. Type: CANADA: Bear Lake to Arctic seacoast, *Richardson s.n.* (holotype: K; isotype: US–865455!, fragment ex K).

Bromus ciliatus var. *coloradensis* Vasey ex Beal, Grass. N. Amer. 2:619. 1896. Type: U.S.A. Colorado: near Gray's Peak, *Wolf 1158* (lectotype: US-1007969!, designated by Hitchcock, Man. Grass. U.S. 816. 1935).

Bromus pumpellianus var. *tweedyi* Scribn. ex Beal, Grass. N. Amer. 2:622. 1896. Type: U.S.A. Montana: Yellowstone Park, Slough Creek, 1885, *F. Tweedy 587* (isotype: US–81592!).

Bromus arcticus Shear in Scribn. & Merr., Contr. U.S. Natl. Herb. 13:83. 1910. *Bromus pumpellianus* var. *arcticus* (Shear) Porsild, Rhodora 41:182. 1939. Type: U.S.A. Alaska: 9 Sep 1901, *F.A. Walpole 2036* (holotype: US–379157!, with the following additional location information: "Vicinity of Port Clarence. Tundra banks near buildings at Teller Reindeer Station").

Perennial; rhizomes present; basal leaves readily decaying into straight fibres. Culms 3.2–4.5 mm wide at base, ± densely pubescent below nodes; nodes 2–3, light brown-yellow, moderately to densely pubescent, hairs to 1 mm long. Leaf sheaths closed for most of their length, glabrous or pilose with long, soft hairs to 2 mm long; auricles present or absent; ligules 1–4 mm long, membranous, glabrous, erose; blades 9–17 cm long, 2.1–10 mm wide, adaxial surfaces glabrous or pubescent with dense, short hairs to 0.5 mm long, abaxial surfaces glabrous or variously pubescent with hairs 0.5–1.2 mm long, hairs sometimes present only marginally, margins serrulate. Panicles 10–29.5 cm long, 1.5–14.5 cm wide, open, branches erect to ascending, shorter or longer than spikelet, scabrous, 1(–2) spikelets per branch, lowest inflorescence node with 4 branches. Spikelets 2.3–3.3 cm long (including awns); florets 7–14. Glumes subequal, lanceolate, glabrous, midnerves scabrous; lower glumes 6.5–10 mm long, 1-nerved; upper glumes 9–12.8 mm long, 3-nerved. Lemmas 10–13 mm long, 1.5–2.6 mm wide, variously pubescent with hairs 0.5–0.8 mm long along margins and midvein or moderately to densely villous throughout; awns 1–4.5(–5) mm long, arising 0–0.5 mm below lemma apex, straight, antrorsely scabrous. Paleas 9.2–11 mm long, shorter than lemmas, cilia present on keels along lower ¾ to entire length, cilia ca. 0.2 mm long. Stamens 3; anthers 4.1–6.5 mm long, yellow to dark brown. $2n = 56$.

Distribution and Habitat.—Native. *Bromus pumpellianus* occurs in western North America from Alaska to New Mexico and west through south-central Alberta, Sasakatchewan and Manitoba to northern Ontario (Pavlick & Anderton 2007). In British Columbia *B. pumpellianus* occurs in the Rocky Mountains (Fig. 12A). Habitat includes grassy banks, grassy meadows, wet banks, sand and gravel bars along rivers and roadsides. Elevation: 597–2000 m.

Common Name.—pumpelly brome.

Notes.—*Bromus pumpellianus* is a morphologically variable taxon. In North America, some authors have treated it as a subspecies or variety of the morphologically similar and putatively closely-related taxon *Bromus inermis* (e.g., Elliott 1949; Wagnon 1952; Scoggan 1978). Several intraspecific taxa have been recognized

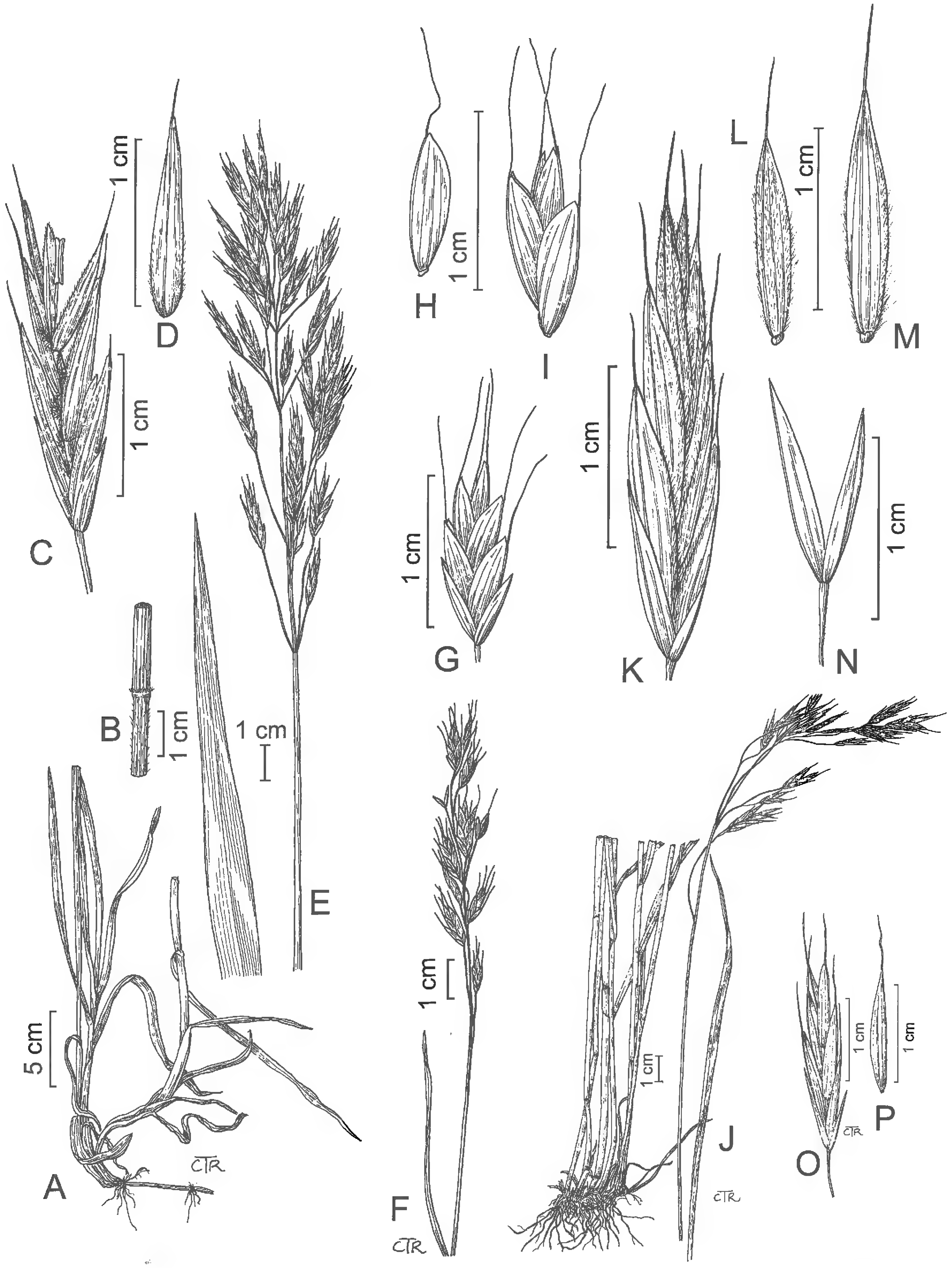

Fig. 11. *Bromus pumpellianus*. A. Rhizome. B. Node. C. Spikelet. D. Lemma. E. Inflorescence. *Bromus racemosus*. F. Inflorescence. G. Spikelet. H, I. Lemmas. *Bromus richardsonii*. J. Inflorescence. K. Spikelet. L, M. Lemmas. N. Glumes. *Bromus riparius*. O. Spikelet. P. Lemma.

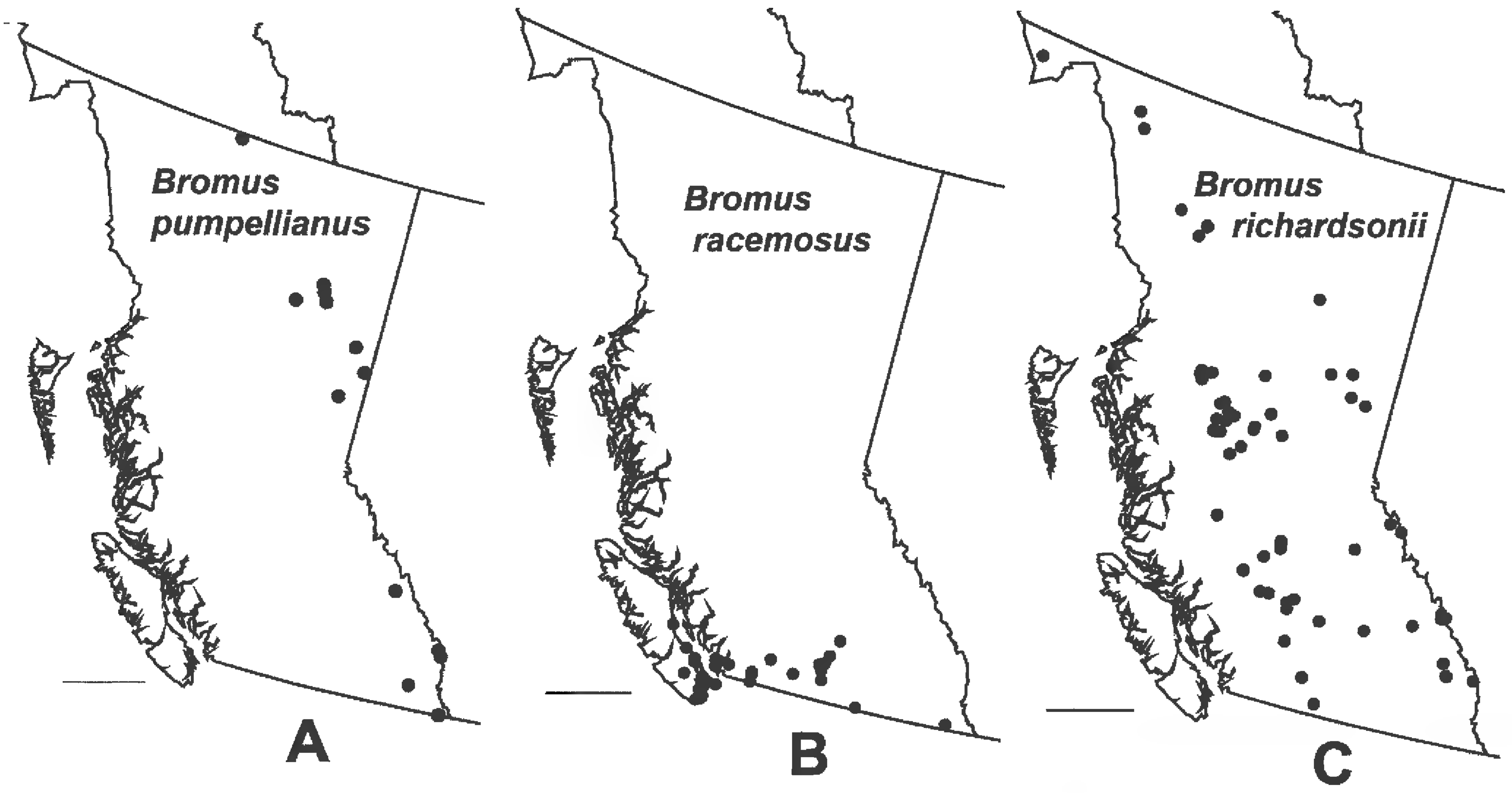

Fig. 12. Geographic distribution in British Columbia. A. *Bromus pumpellianus*. B. *Bromus racemosus*. C. *Bromus richardsonii*. Scale bars = 200 km.

within *B. pumpellianus* based on degree of spikelet pubescence [e.g., var. *arcticus* (Shear) Porsild, var. *purpurascens* (Hook.) Wagnon] but there is substantial intergradation among these types and recent authors do not recognize them (e.g., Mitchell 1967; Pavlick 1995; Douglas et al. 2001; Pavlick & Anderton 2007). *Bromus pumpellianus* is also morphologically similar to the introduced *B. riparius* (see discussion under that taxon).

Representative Specimens Examined. **CANADA. British Columbia:** Moberly, 14 Jul 1930, *R. Graham s.n.* (UBC); vicinity of Sikanni River, 21 Jun 1943, *H.M. Raup & D.S. Correll 10223* (UBC); Perry Creek, Cranbrook (Selkirks), 8 Aug 1943, *J.W. Eastham 11035* (UBC); vicinity of Buckinghorse River, 1 Sep 1943, *H.M. Raup & D.S. Correll 11619* (CAN, UBC); Fort St. John, 23 Jun 1948, *n.c.* (DAO); Ft. St. John, 29 Jun 1949, *V.C. Brink s.n.* (UBC); Mile 98, Haines Road, 7 Jul 1956, *T M.C. Taylor, A.F. Szczawinski & M. Bell 1015* (DAO, UBC), *984* (DAO, UBC), *1035* (DAO); Mile 14, Flathead Rd, 15 Jul 1957, *M. Bell & J. Davidson s.n.* (UBC); Sage Creek Lodge, 21 Jul 1957, *M. Bell & J. Davidson s.n.* (UBC); U.S. Border, Flathead, 4600 ft, 27 Jul 1957, *M. Bell & J. Davidson 599* (UBC); U.S. Border, Flathead, 4600 ft, 27 Jul 1957, *J.W. Eastham 599* (DAO); junction of Goat (Boivin) Creek and Elk River, 4200 ft, 30 Jun 1958, *R.L. Taylor & D.H. Ferguson 2264* (DAO); W of Hyland River at Mile 160, 5 Jul 1960, *J.A. Calder & J.M. Gillett 26541* (DAO); 4 mi NW of Dawson Creek along highway to Ft. St. John, 12 Jul 1960, *J.A. Calder & I. Kukkonen 26820* (DAO); Nevis Creek, 17 Jul 1969, *A. Luckhurst s.n.* (UBC); Nevis Creek, 24 Jul 1969, *A. Luckhurst s.n.* (UBC); Mt Turnbull, Fording River, Creek 4, 29 Sep 1970, *D.C. Morrison s.n.* (UBC); Mt Turnbull, plot 6, Fording River, 28 Jul 1971, *D.C. Morrison s.n.* (UBC); Emkay, Bleasdell Mt, 10 Aug 1972, *n.c.* (UBC); intersection of Ewart Creek and Ashnola River, 9.8.1975, *R. Hainault 7713* (DAO); Robb Lake, slopes on N side of lake, 3900 ft, 29 Jul 1977, *G.W. Argus & E. Haber 10197* (CAN); summit of Pink mountain, 10 Aug 1992, *F. Lomer 92-160* (UBC).

11. Bromus racemosus L., Sp. Pl., ed. 2. 1:114. 1762. (**Fig. 11F–I, 12B**). *Serrafalcus racemosus* (L.) Parl., Rar. Pl. Sic. 2:14. 1840. *Bromus arvensis* var. *racemosus* (L.) Neilreich, Fl. Nieder-Oesterr. 81. 1859. *B. squarrosus* var. *racemosus* (L.) Regel, Act. Hort. Petrop. 7:602. 1881. *Bromus mollis* var. *racemosus* (L.) Bubani, Fl. Pyr 4:387. 1901. *Bromus hordeaceus* var. *racemosus* (L.) Fiori, Nuova Fl. Analitica Ital. 1:149. 1923. Type: *Anon* (lectotype: LINN 93.31, designated by Smith, Notes Roy. Bot. Gard. Edinb. 42:499. 1985).

Annual; rhizomes absent; plants 17–60 tall. Culms 1–2.1 mm wide at base, smooth; nodes 2–3, brown, minutely to densely pubescent, hairs to 0.6 mm long. Leaf sheaths closed for most of their length, densely pubescent, hairs soft and wavy to 1.2 mm long; auricles absent; ligules 0.5–2 mm long, membranous, glabrous, erose; blades 2.7–12 cm long, 1–3 mm wide, adaxial surface densely pubescent with stiff hairs to 0. 8 mm long, abaxial surface densely pubescent with shorter, stiff hairs to 0.6 mm long or like adaxial surface, margins smooth or serrulate. Panicles 3–8.5 cm long (or less when reduced to a single spikelet), 1–2.5 cm wide, longest lower branch < 4 cm long (as measured from node to apex of terminal floret, including awn); branches erect to ascending, sometimes secund, scabrous to pubescent, 1 spikelet per branch, lowest

inflorescence node with 1–4 branches. Spikelets 1.5–2.2(–2.6) cm long (including awns), ovate-lanceolate, rachilla sometimes visible at maturity, florets 6–9. Glumes slightly subequal, smooth or scabrous, keels occasionally serrulate distally; lower glumes 5.2–6.7 mm long, 3–5-nerved; upper glumes 6.2–8.5 mm long, 7–9-nerved. Lemmas 6.5–9.5 mm long, 1.5–2 mm wide, 7–9-nerved, nerves visible but not conspicuously raised, backs glabrous or scabrous to puberulent, hairs to 0.5 mm long, margins ± bluntly angled, apex entire or minutely bifid, the cleft 0.1–0.2 mm deep; awns 3.4–8.5 mm long, arising < 1.5 mm below lemma apex, straight or minutely divaricate, antrorsely scabrous, awns of lowest florets shorter than others. Paleas 5.5-8.5 mm long, shorter than lemmas, backs glabrous, keels ciliate, cilia to 0.3 mm long. Stamens 2; anthers (0.5)1–1.6 mm long, dark brown. $2n = 28$.

Distribution and Habitat.—Introduced. In North America, *B. racemosus* occurs in scattered locations across the U.S.A. and southern Canada (Pavlick & Anderton 2007). In British Columbia *B. racemosus* occurs mostly in the southwestern and southcentral parts of the province (Fig. 12B). Habitats include waste places, field, roadsides and gravelly hillsides. Elevation: 0–967 m.

Common Names.—bald brome, meadow brome, smooth brome, smooth chess.

Notes.—*Bromus racemosus* is often confused with *Bromus hordeaceus* because both taxa have relatively narrow inflorescences, and the two have sometimes been treated as synonyms (e.g., Wilken and Painter 1993). *Bromus hordeaceus* is distinguished by its lemmas with conspicuously raised nerves and generally denser inflorescences. See additional comments under *B. commutatus* and *B. hordeaceus*.

Representative Specimens Examined. **CANADA. British Columbia:** near Victoria, 7 May 1875, *Macoun 29980* (CAN); near Victoria, Aug 1876, *Dawson 29979* (CAN); Nanaimo, 4 Jun 1884, *J. Macoun 29982* (US); Pitt River, Aug 1884, *Macoun 29981* (CAN); Vancouver, 23 Jun 1887, *J. Fowler s.n.* (US); Yale, *Macoun (90)29988* (CAN); Spence's Bridge, 28 May 1889, *Macoun (92)* (CAN); Victoria area, 27 May 1893, *Macoun 116* (CAN); Victoria, 8 Jul 1893, *Wm. Scott s.n.* (DAO); Nanaimo, 20 Jun 1907, *C.O. Rosendahl 1887* (US); vicinity of Victoria, 6 Jun 1908, *J. Macoun 76851* (CAN, US); Robertson River, Vancouver Island, 5 Jul 1911, *W. Spreadborough 87602* (US); vicinity of Sidney, 16 Jun 1913, *J. Macoun 88542* (CAN); Saltspring Island, 24 May 1914, *J.M. Macoun 90094* (CAN); 10th Ave and Willow St., Vancouver, Jun 1918, *J. Davidson s.n.* (UBC); Vernon, 16 Jun 1918, *A.H. Hutchinson s.n.* (UBC); Vernon, 25 Jun 1917, *E.M. Warren s.n.* (UBC); Vernon, 17 Jun 1918, *A.H. Hutchinson s.n.* (UBC); Victoria, Jun 1920, *G.V. Copley 1-15* (UBC); Courtenay, 3 Oct 1930, *H. Groh s.n.* (DAO); Steveston, 20 May 1931, *H. Groh s.n.* (DAO); Saanichton, 27 May 1931, *H. Groh s.n.* (DAO); Ganges, 28 May 1931, *H. Groh s.n.* (DAO); W Point Grey, 14 Jun 1934, *J.W. Eastham s.n.* (UBC); W Point Grey, Vancouver, 20 Jun 1937, *J.W. Eastham s.n.* (UBC); Fairfield Island, Chilliwack, 10 Jun 1946, *J.W. Eastham s.n.* (UBC); Fairfield Island, Chilliwack, 18 Jun 1946, *J.W. Eastham 15133* (DAO); Christina Lake, 29 May 1953, *G.H. Collin s.n.* (DAO); along highway on W side of Skaha Lake between Penticton and Kaleden, 28 Jun 1953, *J.A. Calder & D.B.O. Savile 9784* (US); Christina Lake, 14 Jul 1953, *J.M. Smith s.n.* (DAO); Christina Lake, 31 May 1954, *W.G. Dore & M. Smith s.n.* (DAO); Christina Lake, near Grand Forks, 31 May 1954, *W.G. Dore 15053* (DAO); Parksville, 13 Jul 1954, *T.M.C. Taylor 3086* (UBC); 7 mi N of Duncan, 18 May 1955, *D.R. Lindsay & W. Woodbury 696* (DAO); S Pender Island, 11 Jul 1955, *S. Buchanan s.n.* (UBC); Saltspring Island, 12 Jun 1955, *T.R. Ashlee s.n.* (UBC); Summerland Research Station, 1300 ft, 14 Jul 1960, *A. Mclean 60-83* (DAO); John Dean Park, Saanichton, 1000 ft, 14 Jun 1962, *J. Hett s.n.* (DAO); Henderson Point, W coast of Saanich Peninsula, 14 May 1962, *J. Hett s.n.* (DAO); Uplands Park, Victoria, 15 Jun 1962, *J. Hett 62* (DAO); Gordon Head, Victoria, 19 May 1962, *M. Bell s.n.* (DAO); Beechy Head, 10 ft, 4 Jun 1965, *A. Fisk & B.W. Davies 803* (DAO); Albert Head near Victoria, 30 May 1962, *J. Hett s.n.* (DAO); North Hill, Saanich, 350 ft, 2 Jun 1965, *B.W. Davies & R.A. Keller 752* (DAO); S Kelowna, 14 Jun 1970, *S. Kojima s.n.* (UBC); above Harrison River, 400 ft, 12 Jun 1974, *K.I. Beamish, J. Pinder-Moss, C. Selby, J. Pojar & E. Perkins 74063* (DAO); Patricia Bay Highway, one-half mile N of Royal Oak Corner, 20 May 1955, *D.R. Lindsay & W. Woodbury 754* (DAO); summit of Mount Bruce, S end of Saltspring Island, 3 Jul 1988, *S.J. Darbyshire & J.A. Darbyshire 3777* (CAN); alongside parking lot at UBC Museum of Anthropology, 25 May 05, *J.M. Saarela 305* (CAN, UBC); Rocky Mountain Forest District, along Hwy 3, 1.5 km E of Elko, 23 May 2006, *J.M. Saarela 405A* (CAN, UBC); Osoyoos, Haynes Provincial Park, 25 May 2006, *J.M. Saarela 484* (CAN, UBC); 10 km W of Princeton on Hwy 3, 19 Jun 2006, *J.M. Saarela, C. Sears & J. Maze 586A* (CAN, UBC); ca. 2 km N of Garnet Lake, 14.6 km N on Garnet Valley Road from Hwy 97 at Summerland, 21 Jun 2006, *J.M. Saarela, C. Sears & J. Maze 707* (CAN, UBC).

12. Bromus richardsonii Link, Hort. Berol. 2:281. 1833. (**Fig. 11J–M, 12C**). *Zerna richardsonii* (Link) Nevski, Trudy Sredne-Aziatsk. Gosud. Univ., Ser. 8b, Bot. 17:17. 1934. *Bromus ciliatus* var. *richardsonii* (Link) B. Boivin, Naturaliste Canad. (Que.) 94:521. 1967. *Zerna canadensis* subsp. *richardsonii* (Link) Tzvelev, Novosti Sist. Vyss. Rast. 7:54. 1970 [1971]. *Bromopsis richardsonii* (Link) Holub, Folia Geobot. Phytotax. 8(2):168. 1973. *Bromopsis canadensis* subsp. *richardsonii* (Link) Tzvelev, Zlaki SSSR 214. 1976. Type: Hab. in America septentrionali occidentali. Semina mist cl.: Grown from seed in Berlin, *Richardson s.n.* (holotype: B, destroyed *fide* J. Cayouette & P.M. Peterson 2007).

Bromus purgans var. *longispicatus* Hook., Fl. Bor.-Amer. 2:252. 1840. Type: CANADA: Rocky Mountains, *Drummond s.n.* (isotype: US-A865460!, fragment). Note: Pavlick et al. (2003) included this taxon as a synonym of *B. ciliatus*, but the fragment at US is clearly *B. richardsonii*, on the basis of its glume length and lemma pubescence.

Perennial; rhizomes absent; plants 47–110 cm tall. Culms 1.5–3.5 mm wide at base, smooth; nodes 3–4, brown, glabrous, lower nodes sometimes minutely pubescent. Leaf sheaths closed for most of their length, glabrous or sparsely to densely pilose with stiff hairs 0.2–1.2 mm long; auricles absent; ligules 1–2.5 mm long, membranous, glabrous or minutely pubescent, erose; blades 18.5–34 cm long, 3–9(–13) mm wide, adaxial and abaxial surfaces glabrous, margins smooth or serrulate. Panicles 13–23.5 cm long, 2–17.5 cm wide, open, branches ascending to drooping, shorter or longer than spikelet, smooth-scabrous, 1–5 spikelets per branch, lowest inflorescence node with 1–4 branches. Spikelets 2.4–3.5 cm long, rachilla sometimes visible at maturity; florets 3–9. Glumes subequal, lanceolate, glabrous or minutely pubescent, hairs sometimes restricted to margins, keels glabrous or scabrous; lower glumes 7–9.5(–12) mm long, 1(–3)-nerved, lanceolate; upper glumes (8–)9.5–11.5(–14.5) mm long, 3-nerved, sometimes acuminate or mucronate with mucros to 0.7(–1) mm long. Lemmas 9–13.5(–15) mm long, 2–2.8 mm wide, 7-nerved, pubescent, hairs along margins 0.2–1 mm long, hairs sparsely or densely scattered across the back > 0.1 mm long, apex entire or minutely bifid, the cleft to 0.2 mm long; awns 3.1–6.5 mm long, arising 0–0.5 mm below lemma apex, straight, antrorsely scabrous. Paleas 11–12 mm long, shorter than lemmas, keels glabrous or ciliate, cilia to 0.2 mm long. Stamens 3; anthers 1–2.6(–3.4) mm long, dark brown. $2n = 28$.

Distribution and Habitat.—Native. *Bromus richardsonii* is generally distributed west of the continental divide from the Yukon territory to central Mexico, with disjunct populations known from the Cypress Hills in southern Alberta/Saskatchewan, the Black Hills in South Dakota and western Texas (Peterson et al. 2002; Pavlick & Anderton 2007). *Bromus richardsonii* occurs throughout British Columbia east of the coastal mountain ranges (Fig. 12C). Its distribution is sympatric with that of *B. ciliatus* (Fig. 3B), but *B. richardsonii* generally occurs at higher elevations (Peterson et al. 2002). Habitats include meadows, open woods and gravelly areas. Elevation: 289–2133 m.

Common Name.—Richardson's brome.

Notes.—*Bromus richardsonii* has been variously recognized as a distinct species (Shear 1900; Hitchcock 1913; Wagnon 1952; Mitchell & Wilton 1965; Mitchell 1967; Hultén 1968; Welsh 1974; Pavlick 1995; Herrera Arrieta 2001; Peterson et al. 2002; Saarela et al. 2005; Pavlick & Anderton 2007; Saarela and Peterson, in press), as a synonym of *B. ciliatus* (e.g., Allred 1993; Hitchcock 1951; Soderstrom & Beaman 1968; Wilken & Painter 1993; Douglas et al. 2001) or as a variety of *B. ciliatus* (e.g., Kartesz 1999). In a detailed study of the complex, Peterson et al. (2002) identified distinctive morphological, cytological and genetic differences that support recognition of these taxa as distinct species (see Taxonomic Key).

Representative Specimens Examined. **CANADA. British Columbia:** Sicamous, 3 Jul 1889, *Macoun 30013* (CAN); below Wapta Lake, Rocky Mts, 6 Aug 1904, *Macoun 64804* (CAN); Field, Rocky Mountains, 19 Aug 1904, *Macoun 64803* (CAN); Sicamous, 16 Jul 1914, *M. Malte s.n.* (CAN, DAO); near Bow River, Field, 1-2 Aug 1914, *A. S. Hitchcock 11537* (US); Field, 2 Aug 1914, *A.S. Hitchcock s.n.* (DAO); E of Field, 1-2 Aug 1914, *A.S. Hitchcock 11,552* (US); Sinclair Hot Springs, 2 Aug 1915, *M.O. Malte s.n.* (CAN, DAO); Prince Rupert, 1 Aug 1916, *M.O. Malte s.n.* (CAN); W and NW slopes of Mt Selwyn, 4000 ft, 26 Jul 1932, *H.M. Raup & E.C. Abbe 4160* (CAN); Burns Lake, 5 Jul 1935, *O.J. Murie 2588* (US); Watching Creek, Tranquille, 8 Jul 1936, *E.W. Tisdale 6902* (DAO, UBC); Telkwa, 30 Jul 1937, *J.D. Menzies s.n.* (UBC); Callanah Lake, Riske Creek, Chilcotin, 14 Aug 1938, *H.A. Senn 1941* (UBC); Fairmont Hot Springs, 16 Jul 1941, *J.W. Eastham s.n.* (UBC, V); Mt Stephen area, Yoho National Park, 1 Aug 1943, *W.C. McCalla 7807* (UBC); valley of Kicking Horse River, 3 mi E of Field, 14 Sep 1943, *G.H. Turner 3833* (DAO); Fort St. James, 3 Jul 1944, *J.W. Eastham s.n.* (UBC); Ootsa Lake P.O., 8 Jul 1944, *J.W. Eastham s.n.* (UBC); Burns Lake, 16 Jul 1944, *J.W. Eastham s.n.* (CAN, UBC, V); Canoe Creek, Clinton area, 8 Aug 1946, *C. Rogers 35* (DAO); Pavilion Lake, 29 Aug 1949, *V.C. Brink 49-470* (UBC); ca. 5 mi on Gibson Pass rd to Paddy Lake, Manning Park, 28 Jul 1960, *A. McLean s.n.* [60-203?] (DAO); Chilcotin, plot no. 90, 3650 ft, Jul 1968, *C. Beil 68-7-17* (UBC); Chilcotin, plot no. 110, Aug 1968, *C. Beil 68-8-19* (UBC); area of 10 mile Carbon Creek, 18 Aug 1971, *n.c.* (UBC); Emkay, Bleasdell Mt, 10 Aug 1972, *n.c.* (UBC); near Fraser Lake, NW of Drywilliam Lake, 2450 ft, 10 Aug 1973, *V.J. Krajina & R. Revel s.n.* (UBC); ridge, 1.5 mi SE of Tyhee Lake, 2300 ft, 14 Jul 1974, *V.J. Krajina, J. Pojar & C. Parsons s.n.* (UBC); Ashnola Road, mile 24, 29 Jul 1975, *R. Hainault 7630* (DAO); Driftwood Creek, ca. 7 mi ENE of Smithers, 2400 ft, 17 Jul 1974, *V.J. Krajina, J. Pojar & C. Parsons s.n.* (DAO, UBC); Driftwood Canyon and Smithers, 19 Jul 1974, *J. Pojar J.92* (UBC); above Salix Creek, vicinity of mouth of Cow Parsnip Creek, Gladys Lake area, 4700 ft, 3 Aug 1975, *J. Pojar s.n.* (UBC); W entrance to Sanctuary Pass, Gladys Lake area, 5000 ft, 19 Aug 1975, *J. Pojar s.n.* (UBC); ca. 1 mi E of Relay Creek Cabin, 18 Jul 1977, *C. Selby plot 35 #399* (UBC); White Horse Bluffs area, S of Wells Gray Park, 25 Jul 1979, *T. Goward 81-375* (DAO); Bissett Creek, 10 km SW of Chetwynd, 610 m, 3 Aug 1979, *L.E. Pavlick 79-779* (V); Stones Bay Road, 7 km from Post Office, Fort St. James, 13 Jul 1981, *A. Kruckeberg 101* (UBC); Beece Creek area, 1510 m, 10 Aug 1981, *L.E. Pavlick 81-113* (V); Chilcotin area, Big Creek – Farwell Canyon road, near Big Creek, 14 Sep 1993, *J. Cayouette 7620* (DAO); Chilcotin Mts, Taseko Lake area, close to Beece Creek, 15 Sep 1993, *J. Cayouette*

7621 (DAO); Road 5A, 1 km N of Borgeson Lake, 16 Sep 1993, *J. Cayouette 7622* (DAO); Pope Mountain, near Ft. St. James, 792 m, 19 Jul 1996, *J.L. Penny & Botany BC 1996* (UBC); 13 mi SW of Clinton just past Kelly Lake, 26 Jul 2004, *P.M. Peterson, J.M. Saarela & S. Smith 18740* (CAN, US); 1 mi S of Iskut on Hwy 37 towards Meziadin Junction, along Coyote Creek, 20 Jul 2004, *P.M. Peterson, J.M. Saarela & S. Smith 18675* (CAN, US); Skihist Provinical Park, Hwy 8, ca. 10 km from Lytton, 22 Jun 2006, *J.M. Saarela, C. Sears & J. Maze 728* (CAN, UBC); 5.5 km along North Shore Road (Stella Road), N of Hwy 16, just W of Nadleh Whuten Band First Nation Reserve boundary, N of Fraser Lake, 18 Jul 2007, *J.M. Saarela & D.M. Percy 1068* (CAN, UBC); along Jeanine Road, N shore of Fraser Lake, ca. 100 km W of Prince George, along dirt road 12 km W of Nadleh Whuten Band First Nation reserve, area known locally as "Red Beach", 18 Jul 2007, *J.M. Saarela & D.M. Percy 1083* (CAN, UBC); old gravel mining area, just S of Hwy 16, N of Bulkley River, just E of Ross Lake, 19 Jul 2007, *J.M. Saarela & D.M. Percy 1089* (CAN, UBC).

13. Bromus riparius Rehm., Notiz. Veg. Gest. Schwartz Meer 83. 1872. (**Figs. 11O–P, 13A**). *Zerna riparia* (Rehm.) Nevski in Acta Univ. Asiae Med. Ser. 8b, Bot. 17:17. 1934. *Bromopsis riparia* (Rehm.) Holub, Folia Geobot. Phytotax. 8:169. 1973. *B. biebersteinii* auct. Am., *non* Roem. & Schult. Type: RUSSIA: *Rehmann s.n.* (isotype: LE).

Perennial; caespitose with short rhizomes; decaying basal leaves reticulate-fibrillose, plants 34–120 cm tall. Culms 2.8–6 mm wide at base, smooth; nodes (2–)3–4, brown, smooth or pubescent with hairs 0.2–0.5 mm long. Leaf sheaths closed for most of their length, glabrous to moderately pubescent with soft, wavy hairs to 0.5–1.6 mm long; auricles absent; ligules 1.1–3 mm long, membranous, glabrous, erose; blades 11.5–32 cm long, 2–6.5 mm wide, adaxial surfaces glabrous or sparsely to densely pilose with hairs 0.5–2.5 mm long, abaxial surfaces pubescent with short hairs 0.3–0.5 mm long or longer hairs to 2 mm long, margins with robust, stiff hairs to 2.5 mm long that are widest at the base. Panicles 5.5–23 cm long, 1.5–10 cm wide, open, branches erect to ascending, branches shorter or longer than spikelet, scabrous, 1–3 spikelets per branch, lowest inflorescence node with (1)2–3 branches. Spikelets 1.9–3.6 cm long (including awns); florets 4–10. Glumes subequal, lanceolate, glabrous or sometimes pubescent with hairs to 0.7 mm long, hairs sometimes restricted to nerves; lower glumes 6–9.7 mm long, 1-nerved; upper glumes 7.5–11 mm long, 3-nerved. Lemmas 11–13 mm long, 1.3–1.6 mm wide, glabrous or pubescent throughout or marginally, hairs to 0.5(–1) mm long, midribs scabrous distally; awns 3.5–7.1 mm long, arising 0–1 mm below lemma apex, straight, antrorsely scabrous. Paleas 9–9.6 mm long, shorter than lemmas; keels ciliate along upper half to 2/3 of their length, the cilia 0.1–0.2 mm long. Stamens 3; anthers (3–)4–5.7 mm long; dark brown to orange. $2n = 70$.

Distribution and Habitat.—Introduced. Grassy meadows, pastures. *Bromus riparius* is known only from a single collection along Highway 3 in southeastern British Columbia (Fig. 13A). It is promoted in western North America for forage, but its precise distribution is not clear (Pavlick & Anderton 2007). See additional notes below.

Common Name.—English: meadow brome; French: brome des prés.

Notes.—Meadow brome (*Bromus riparius*) is native to southeastern Europe, Turkey, the Caucasus and central Asia. It was introduced into North America in the last century as a potential forage crop. A cultivar ('Regar') selected from material collected in Turkey was registered in the United States in 1966 and in Canada in 1980 (de Araújo & Coulman 2004). *Bromus riparius* is now promoted and grown widely for forage across western Canada and in adjacent regions of the U.S.A. There is substantial interest in this grass in the agronomic community and several cultivars ('Fleet', 'Paddock', 'Cash' and 'Montana') have recently been developed (Knowles 1990a, b; Cash et al. 2002; Jensen et al. 2004). From its first release, the name applied (incorrectly) to meadow brome in the United States was *B. biebersteinii* Roem. & Schult., a name that is still widely used in many government agronomy publications and in the seed trade. *Bromus biebersteinii* is a morphologically distinct Eurasian species (Tzvelev 1976) that is not reported for North America.

Bromus riparius is morphologically similar and closely related (Saarela et al. 2007) to *B. inermis* (smooth brome; see above), another introduced species widely used for forage and hay, which is seriously invasive in native plant communities (Otfinowski et al. 2007). Smooth bromegrass is widely grown because it is drought-tolerant and sod-forming, but it has slow regrowth characteristics and is considered better suited for use as hay. Meadow brome has better re-growth characteristics and is thus considered better suited for forage in pasture conditions (e.g., Thompson et al. 2003). Several reports indicate that *B. riparius* is less

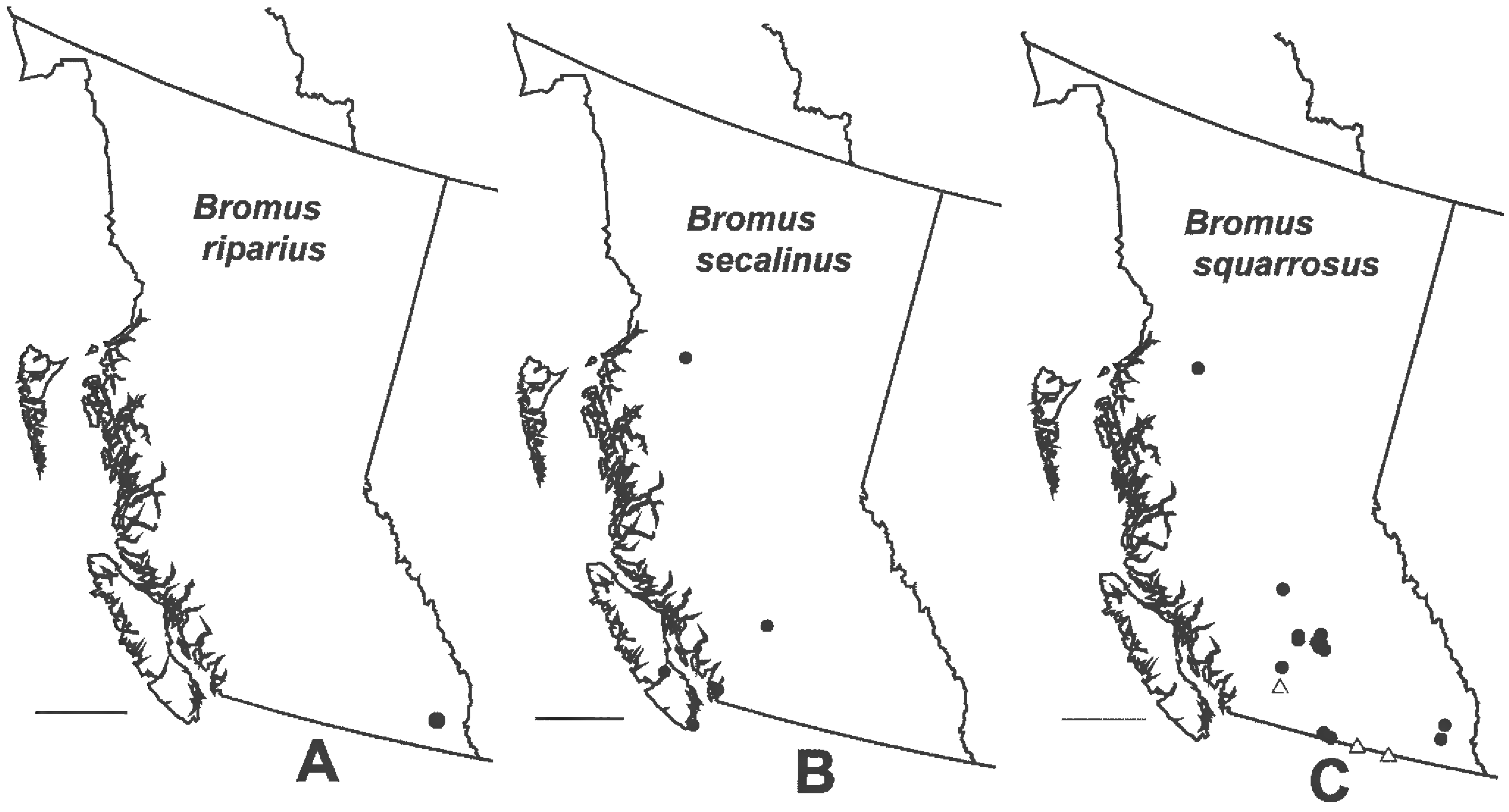

Fig. 13. Geographic distribution in British Columbia. A. *Bromus riparius*. B. *Bromus secalinus*. C. Circles: *Bromus squarrosus* var. *squarrosus*; triangles: *Bromus squarrosus* var. *villosus*. Scale bars = 200 km.

aggressive than *B. inermis* and not invasive (Anonymous 2000; de Araújo 2001; Ogle et al. 2004). Through breeding efforts, two hybrid bromegrasses have been developed and selected by Agriculture and Agri-Food Canada: one originating from a cross between *B. inermis* and *B. riparius* ('Knowles'; Coulman 2004), the other originating from a *B. inermis* × *B. riparius* hybrid backcrossed with *B. inermis* ('Success'; Coulman 2006). These hybrids combine characteristics of each of their parents; they are considered suitable for use as both hay and pasture (Knowles & Baron 1990; Knowles et al. 1993; Coulman 2004, 2006). Because of their agricultural importance, numerous aspects of morphology, forage quality and genetic diversity have been characterized in *B. inermis*, *B. riparius*, and their hybrids (e.g., Ferdinandez and Coulman 2000, 2001, 2002; Ferdinandez et al. 2001; de Araújo & Coulman 2004). There are no reports of *B. riparius* being adventive in Canada.

Bromus riparius was treated in the Flora of North America (Pavlick & Anderton 2007). It was included there shortly before the volume went to press, but a detailed distribution map for the taxon was not available. In Canada, *Bromus riparius* is recognized as part of the flora in Saskatchewan (determined incorrectly as *B. biebersteinii* Roem. & Schult.; Harms 2006). Almost certainly it is present in Alberta, and a recent collection from Manitoba is cited below. It has not yet been reported for British Columbia. There is no mention of *B. riparius* (or *B. biebersteinii*) in recent treatments of the British Columbia flora (Qian & Klinka 1998; Douglas et al. 2001), nor in Pavlick's (1995) treatment of *Bromus* in North America. In May 2006 I collected *B. riparius* in southeastern British Columbia in a fenced-in meadow at a rest stop along Hwy 3 [*Saarela 417* (CAN, UBC)]; this collection apparently represents the first record of the species in the province. Indeed, the species has been grown in field trials in British Columbia (e.g., at Devick near Kamloops; May et al. 1999), and cultivars of *B. riparius* are promoted for forage in British Columbia and used for amelioration (S. J. Darbyshire, pers. comm., March 2007; see http://www.agf.gov.bc.ca/forage/factsheets.htm). *Bromus riparius* may have been deliberately planted here as forage, or it may have been introduced by road traffic. Seed of *B. riparius* is sometimes found as a contaminant in smooth brome seed commodities (Allison et al. 2001; S.J. Darbyshire, pers. comm. March 2007). Whatever the source of the introduction, *Bromus riparius* should be recognized as a component of the British Columbia flora, and additional occurrences for this species should be looked for.

The morphological description is based on my field collections from British Columbia and Manitoba, as

well as several specimens of cultivated plants (mostly greenhouse grown at the Agriculture and Agri-Food Canada Central Experimental Farm in Ottawa, Ontario, Canada) in DAO. Some of this cultivated material represents the cultivars 'Fleet,' 'Paddock' and 'Regar'; differentiating morphologically among these and the other cultivars was beyond the scope of this study. *Bromus riparius* is one of three *Bromus* species in British Columbia (including *B. inermis* and *B. pumpellianus*) with rhizomes and long anthers (usually > 4 mm), and it therefore is relatively straight forward to identify. These three species are members of an Old World alliance of taxa (*B. pumpellianus* is the only native species in North America that is part of this group) whose evolutionary relationships with other North American perennial *Bromus* species are not yet clear (Saarela et al. 2007). Because *B. riparius* is a relatively recent addition to the New World flora, there is little information in the North American botanical taxonomic literature for the species.

There are several morphological characters that distinguish *Bromus riparius*. In an effort to identify characteristics to help seed analysts distinguish florets of *B. inermis* and *B. riparius*, which are sometimes mixed in seed commodities, Allison et al. (2001) conducted a careful study of the floret morphology of these taxa and found useful variation in the cilia (described by them as 'siliceous prickle hairs') on the palea keels. In *B. riparius*, cilia on the palea keels are present only distally, whereas in *B. inermis* cilia are present on the keels along the entire palea length. Figures 1–4 and 9 in Allison et al. (2001) illustrate this character clearly. Allison et al. (2001) did not examine this character for *B. pumpellianus*. In *B. pumpellianus* cilia are present along the entire length of the palea keels, like in *B. inermis*, or only along the lower ¾. *Bromus riparius* is further distinguished by its longer awns, which are (3–)4–7.1 mm long [vs. 0–3 mm long in *B. inermis* and 1–4 mm long in *B. pumpellianus*]. Several vegetative characters are also useful in distinguishing the three species. Leaf blade margins of *B. riparius* are characterized by the presence of long, stiff hairs (to 2.5 mm long) that are conspicuously wider at their base (Fig. 14); such robust hairs do not occur in *B. inermis* and *B. pumpellianus*. In his keys to *Bromus* in the (former) U.S.S.R., Tzvelev (1976) distinguished *B. riparius* from *B. inermis* and *B. pumpellianus* by the degree of shredding of basal leaf sheaths. Examination of this character in Canadian material confirms that it is very useful for distinguishing *B. riparius* from the other two taxa. The basal sheaths of decaying leaves in *B. riparius* are reticulate-fibrillose (i.e., they have a 'thatched' appearance), the readily decaying basal sheaths in *B. pumpellianus* are split into straight fibers and the basal sheaths of *B. inermis*, which do not appear to decay as readily as those in *B. pumpellianus* or *B. riparius*, also split into straight fibers (Fig. 15). Pavlick & Anderton (2007) distinguished *B. riparius* from *B. inermis* and *B. pumpellianus* based on culm height and rhizome length; they noted that time constraints did not allow them to fully clarify its similarities and differences with these other taxa. *Bromus riparius* is weakly rhizomatous, *B. pumpellianus* is moderately so and *B. inermis* is strongly rhizomatous. Pavlick & Anderton (2007) also noted that it is not clear how *B. riparius* differs from *B. pumpellianus* subsp. *dicksonii* W. W. Mitch. & Wilton, a taxon known only from the Yukon River drainage in northwestern North America (Yukon and Alaska); characterization of differences between these two taxa was beyond the scope of this study.

Representative Specimens Examined. **CANADA. British Columbia:** Rampart Rest Area, 10 km E of Cranbrook, meadow under *Pinus ponderosa* and *Juniperus scopulorum*, 49°33"2'N 115°8"38' W, 856 m, 23 May 2006, *J.M. Saarela 417* (CAN, UBC). **Alberta:** Lethbridge, 10.15.1987, *S. Smoliak s.n.* (DAO-540342); cultivated land, fallow, NE-19-42-10-W4, 10 mi S of Hardisty, 3 Jun 1993, *T. Yorchak V93W-FC268* (DAO-67859). **Manitoba:** Mary Jane Reservoir, ca. 10 km NW of Manitou, open, relatively undisturbed prairie habitat S of the reservoir, 14 Jul 2007, *J.M. Saarela 1001* (CAN). **Ontario (cultivated):** Ottawa, Central Experimental Farm, greenhouse, cv. Fleet, 7 Aug 1992, *S.J. Darbyshire s.n.* plant #28 (DAO-668498), plant #17 (DAO-668495), plant #25 (DAO-668496), plant #8 (DAO-668494), plant #9 (DAO-668493), plant #27 (DAO-668497), plant #31 (DAO-668500), plant #29 (DAO-668499); Ottawa, Central Experimental Farm, greenhouse, cv. Fleet, planted 26 Nov 1996, received as breeder seed C-86-2778, accession number 183, 22 Nov 1997, *M. Murray s.n.* (DAO-747661); Ottawa, Central Experimental Farm, collected from greenhouse, cv. Fleet, source: seed and rootstalks sent by R.P. Knowles in late 1987 from Saskatoon, 15 Apr 1988, *S.J. Darbyshire s.n.* (DAO-575082); grown at Saskatchewan, Saskatoon, cv. Fleet, received in Ottawa as live plant 17 Sep 1987, *R.P. Knowles # Fleet PH 12-5* (DAO-547672); grown at Saskatchewan, Saskatoon, cv. Fleet, received in Ottawa as live plant, 17 Sep 1987, *R.P. Knowles # Fleet PH 12-32* (DAO-547670); Ottawa, Central Experimental Farm, greenhouse, cv. Paddock, 7 Aug 1992, *S.J. Darbyshire s.n.* plant # 19 (DAO-668488), plant #31 (DAO-668492), plant #30 (DAO-668490), plant #10 (DAO-668487), plant #17 (DAO-668486), plant #27 (DAO-668489), plant #32 (DAO-668491); Ottawa, Central Experimental Farm, greenhouse grown, cv. Paddock, 23 Oc 1991, *S.J. Darbyshire 4337* (DAO); Ottawa, Central Experimental Farm, greenhouse, cv. Regar, planted 26 Nov 1996, received as breeder seed C-94-2023, 10 Nov 1997, *M. Murray s.n.* (DAO-74330); Ottawa, Central Experimental

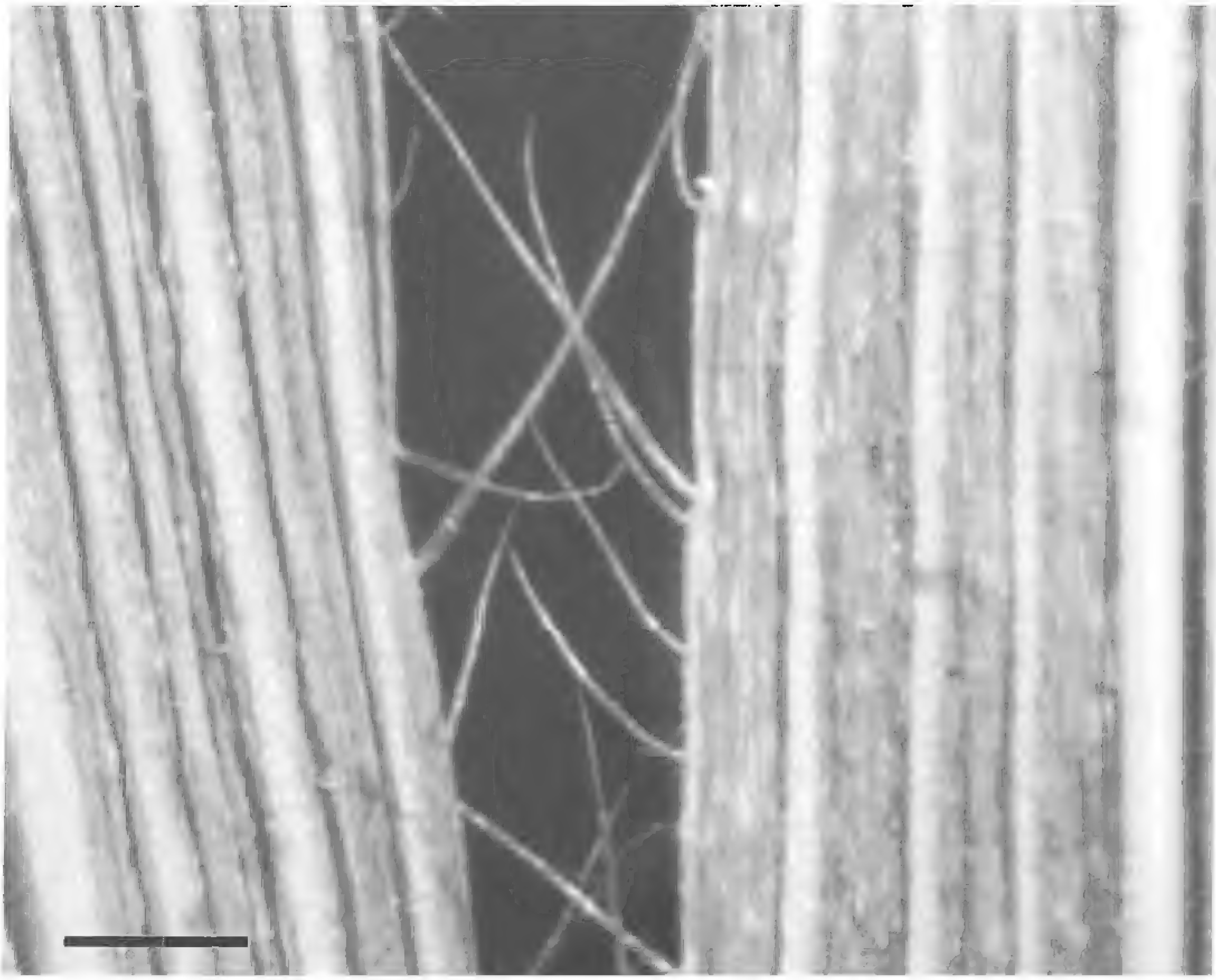

Fig. 14. Leaf blades of *Bromus riparius* [*Saarela 417* (CAN)], showing the long, robust marginal hairs that characterize the species. Scale bar = 1.5 mm.

Farm, greenhouse, cv. Paddock, planted 26 November 1996, received as breeder seed C-86-2787, accession number 182, 26 Oct 1998, *M. Murray s.n.* (DAO-747653); Ottawa, Central Experimental Farm, cold frames, 23 Jun 1989, *S.J. Darbyshire s.n.* (DAO-594764, DAO-593967). **UNITED STATES OF AMERICA. WASHINGTON:** Cultivated at ARS-Pullman [from seeds (PI Identifier 31587) collected at: Russian Federation, Stavropol, Stavropol Territory, 16 Jun 1966, *N. I. Vavilov, All-Russian Scientific Research 2*], 14 Aug 1996, *S.M. Saufferer s.n.* (DAO-594935).

14. Bromus secalinus L., Sp. Pl. 1:76. 1753. (**Figs. 16A–E, 13B**). *Bromus mollis* var. *secalinus* (L.) Huds., Fl. Angl., ed. 2. 2:49. 1778. *Avena secalina* (L.) Salisb., Prodr. Stirp. Chap. Allerton 22. 1796. *Serrafulcus secalinus* (L.) Bab., Man. Brit. Bot. 1:374. 1843. *Forasaccus secalinus* (L.) Bubani, Fl. Pyren. 4:388. 1901. Type: EUROPE: habitat in Europae agris secalinis arenosis, *Anon.* (neotype: LINN-93.1, designated by P.M. Smith, Notes Roy. Bot. Gard. Edinburgh 42:498. 1985).

Bromus submuticus Steud., Syn. Pl. Glumac. 1:351. 1854. Type: U.S.A. Missouri: St. Louis, 1838, *N. Riehl s.n.* (isotype: US-865472, fragment).

Annual; rhizomes absent. Culms 23–130 cm tall, 1–5(–7) mm wide at base, smooth; nodes 3–5, blackish-brown to yellow-brown, finely to densely retrorsely pubescent, hairs 0.1–0.4 mm long, lower nodes covered by sheaths. Leaf sheaths glabrous or sparsely pilose, hairs soft, 0.5–0.6 mm long; auricles absent; ligules 1.7–2.8 mm long, membranous, glabrous, apex erose; blades 8–28.5 cm long, 2–9 mm wide, abaxial surface pilose, hairs to 1.5(–2) mm long, soft and wavy, adaxial surface glabrous with occasional hairs to 0.5 mm long, margins smooth. Panicles 11–22 cm long, 2–9 cm wide, open, branches stiffly erect, sometimes secund, one or more lower branches usually longer than spikelet, smooth to scabrous, 1–3 spikelets per branch, lowest inflorescence node with 1–6 branches; 6–36 spikelets. Spikelets 1.3–2.5 cm long, ovate-

Fig. 15. Pattern of decay in basal leaf sheaths. A. *Bromus riparius* [*Saarela 417* (CAN, UBC)]. Basal sheaths decay readily and are reticulate-fibrillose. B. *Bromus inermis* [*Brink s.n.* (UBC-V215195)]. Basal leaf sheaths do not decay readily; when they do decay, they split into straight fibers. C. *Bromus pumpellianus* [*n.c.* (UBC-V221751)]. Basal leaf sheaths readily decay into straight fibers. Scale bars = 1.5 mm.

lanceolate, terete to slightly compressed, rachilla zigzagged and visible at maturity, florets 5–12. Glumes slightly subequal, smooth or scabrous, keels occasionally serrulate distally; lower glumes 3.6–4.9 mm long, 3–5(–7)-nerved; upper glumes 4.2–6.1 mm long, 7-nerved, sometimes mucronate, mucros 0.2–0.6 mm long. Lemmas 6–7.7 mm long, 1.6–3 mm wide, 7–9-nerved, nerves not conspicuous, ovate-lanceolate, backs glabrous and shiny, occasionally scabrous distally, margins dinstinctly inrolled in fruit; apex entire or minutely bifid, the cleft 0.1–0.2 mm deep; awns 1–6.5 mm long, occasionally reduced to mucro or absent, arising 0.5–0.7 mm below lemma apex, usually straight, occasionally twisted once near base, widest at base, antrorsely scabrous. Paleas ± equal in length to lemmas, apex usually visible at lemma summit, backs glabrous, keels ciliate, cilia to 0.3 mm long. Stamens 2; anthers 1–1.3 mm long, dark brown. Caryopses U- or V-shaped (i.e., margins strongly infolded) in cross section. $2n = 28$.

Distribution and Habitat.—Introduced. In North America, *B. secalinus* has been collected throughout the U.S.A. and southern Canada. It is apparently absent from the Canadian prairie provinces. In the U.S.A. it is most common in the midwestern states (Pavlick & Anderton 2007). *Bromus secalinus* has been collected only a few times in British Columbia, mostly in the southwestern part of the province (Fig. 13B); the most recent collection is from 1991. Habitat includes waste places and fields.

Common Names.—English: cheat, cheat chess, cheat grass, chess, chess brome, ryebrome, rye brome; French: brome des seigles, brome sécaline, coquiole noire, séglin, seigle bâtard, brome faux seigle, seiglin.

Representative Specimens Examined. **CANADA. British Columbia:** Hazelton, [date illegible], *G. Gervais s.n.* (UBC); Alberni, 1900, [collector illegible] (V); Vancouver Island, district of Renfrew, 19 Jul 1902, *C.O. Rosendahl 787* (CAN); Beacon Hill, 22 Jul 1913, *J. Macoun s.n.* (V); within 5 mi of Lillooet, 7 Jul 1916, *J.M. Macoun 93,964* (CAN, V); Swan Lake, Vancouver Island, 13 Jul 1938, *J.W. Eastham s.n.* (UBC); New Westminster, 12 Jul 1991, *F. Lomer 91-149* (UBC).

KEY TO THE VARIETIES OF *BROMUS SQUARROSUS*

15a. Glumes and lemmas glabrous or scabrous ____ **B. squarrosus** var. **squarrosus**

15b. Glumes and lemmas densely pubescent, hairs to 0.8 mm long ____ **B. squarrosus** var. **villosus**

15a. Bromus squarrosus L. var. **squarrosus**, Sp. Pl. 1:76. 1753. **(Figs. 13C, 16F–I)**. *Serrafalcus squarrosus* (L.) Bab., Man. Brit. Bot. 375. 1843. *Forasaccus squarrosus* (L.) Bubani, Fl. Pyren. 4:385. 1901. *Bromus japonicus* var. *paniculatus* (Kuntze) Roshev., Fl. Turkmen. 1:171. 1932. Type: SPAIN: *Loefling 79a* (lectotype: LINN-93.8, designated by Smith, Notes Roy. Bot. Gard. Edinb. 42:500. 1985).

Annual; rhizomes absent; plants 10–43 cm tall. Culms 1–2 mm wide at base, smooth; nodes 2–3, dark brown, pubescent, hairs to 0.6 mm long. Leaf sheaths closed for most of their length, open for 4.2–9 mm

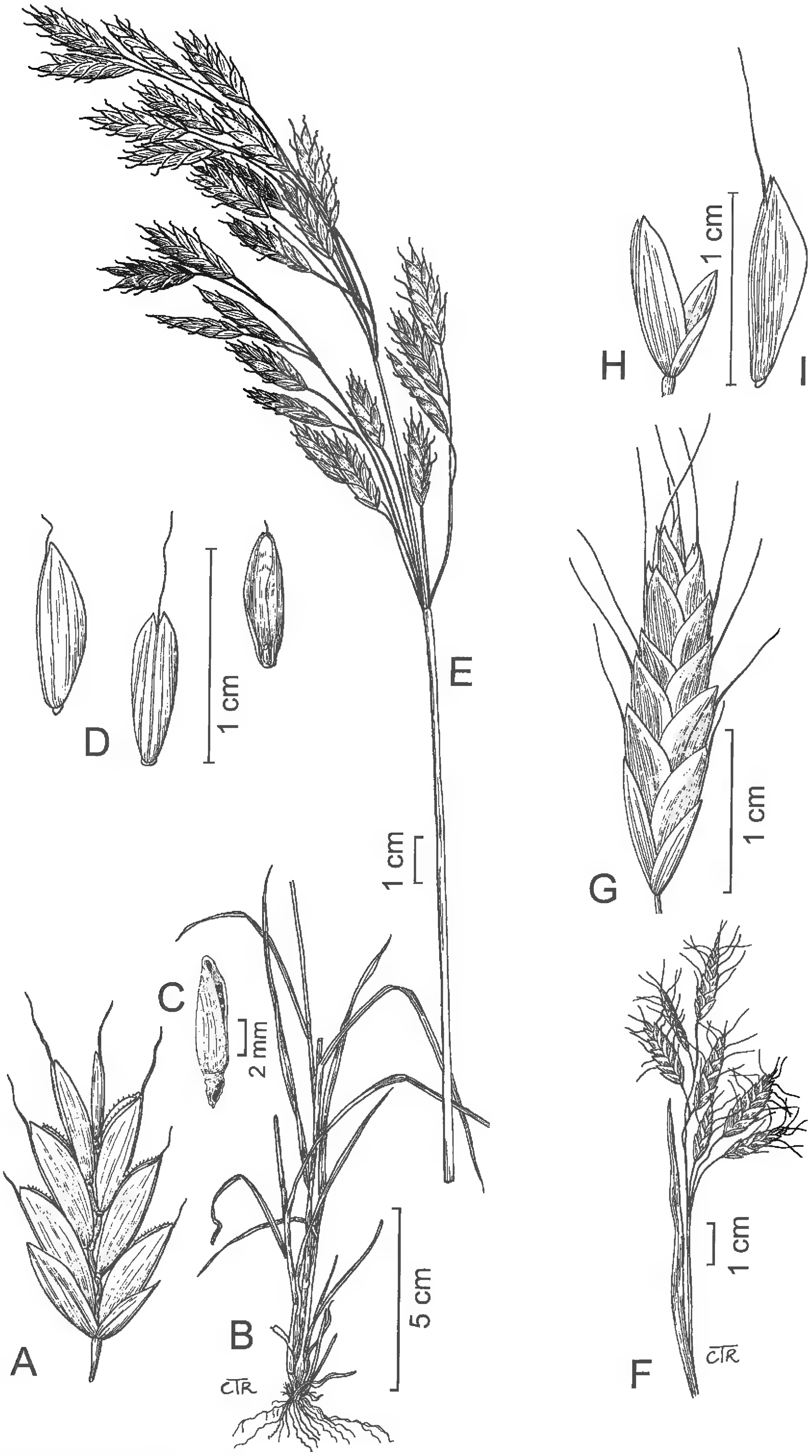

Fig. 16. *Bromus secalinus*. **A.** Spikelet. **B.** Habit. **C.** Caryopsis. **D.** Lemmas. **E.** Inflorescence. *Bromus squarrosus*. **F.** Inflorescence. **G.** Spikelet. **H.** Glumes. **I.** Lemma.

near apex, densely pilose with soft or sometimes stiff hairs 0.5–2 mm long; auricles absent; ligules 0.5–2 mm long, membranous, pubescent, apex erose; blades 2.5–10 cm long, 1.5–3 mm wide, abaxial surface densely pubescent, hairs 0.5–1.5 mm long, adaxial surface glabrous or minutely to densely pubescent, hairs stiff and short or like abaxial surface than, margins smooth or serrulate. Panicles (5–)7–10.5 cm long, 2.7–7 mm wide, open, lax and somewhat sparse, racemose, often appearing one-sided (secund), sometimes reduced to a single spikelet, one or more lower branches usually longer than spikelet, branches smooth to scabrous, 1(–2) spikelets per branch, lowest inflorescence node with 1–4(–5) branches; 3–17 spikelets. Spikelets 1.4–3.5 cm long, broadly oblong to ovate-lanceolate, terete to moderately compressed, rachillas not visible at maturity, florets 7–18. Glumes subequal, smooth, margins sometimes hyaline; lower glumes 4.5–7 mm long, 3–5(–7)-nerved; upper glumes 6.1–9.5 mm long, 7-nerved. Lemmas 8.2–11 mm long, 1.8–3.1 mm wide (when compressed), 7–9-nerved, nerves not conspicuous, broadly obovate, strongly angled near the middle, backs glabrous or scabridulous or (rarely) densely pubescent with hairs to 0.5 mm long, hyaline margins 0.5–1.2 mm wide at widest point, puberulent, apex minutely bifid, the cleft 0.1–0.3 mm deep; awns 8–11.7 mm long (awn on lowest lemma shorter), arising 1.7–3 mm below lemma apex, strongly divergent, usually twisted once near base, widest at base, scabrous. Paleas 6.1–9 mm long, backs glabrous, keels ciliate, cilia 0.3–0.5 mm long. Stamens 2; anthers (0.5–)0.9–1.6 mm long, dark brown. $2n = 14$.

Distribution and Habitat.—Introduced. *Bromus squarrosus* var. *squarrosus* is native to Eurasia (Tzvelev 1976). In North America it occurs across the Great Plains in the northern U.S.A., around the Great Lakes area and in other scattered locations (Pavlick & Anderton 2007). In British Columbia it is most common in the interior and in the Columbia basin (Fig. 13C). Habitats include grasslands, hillsides, disturbed areas and roadsides. Elevation: 311–823 m.

Common Names.—corn brome, downy brome, field brome, nodding brome, one-way brome.

Representative Specimens Examined. **CANADA. British Columbia:** near Kamloops, 2000 ft, 27 May 1934, *G. V. Copley 7* (DAO); Richter Pass, Jul 1936, *E.W. Tisdale 8850* (UBC); Kamloops, 22 Jun 1939, *E.W. Tisdale 8759* (UBC); Lac du Bois, Kamloops, 4 Aug 1939, *E.W. Tisdale 8760* (UBC); Kamloops, Sep 1939, *E.W. Tisdale 8761* (UBC); Lac du Bois, Kamloops, 2700 ft, 10 Aug 1939, *E.W. Tisdale 40-8* (DAO); Ashcroft, 6 Aug 1950, *V.J. Krajina s.n.* (UBC); Tranquille, 1100 ft, 5 Oct 1962, *V.C. Brink s.n.* (UBC); Bonaparte River Valley, 15 mi N of Cache Creek, 1200 ft, 20 Jun 1965, *V.J. Krajina 65062007* (UBC); St. Eugene Mission, Cranbrook, 23 Jun 1968, *F. Fodor 647* (UBC); Kamloops, Lac du Bois Range behind Research Station, 23 Jun 1980, *S.G. Aiken 1071* (DAO); Dallas Cliff (Point), 17 Jun 1982, *R.K. Scagel 82-28* (UBC); N of Copper Creek, towards Tranquille Lake, 9 Jul 1991, *F. Lomer 91-139* (UBC); Kootenay, Wasa, 20 Jun 1993, *L.E. Pavlick 93-044* (V); Cariboo-Chilcotin, Dog Creek area, Harper's Creek Valley (S of creek), 3 Jul 1994, *T. Goward & C. Clement 94-377* (UBC); Anarchist Mt, E of Osoyoos near Hwy 3, 15 Jul 1994, *F. Lomer 94-152* (UBC); near border of N end of Yale region and S end of Kamloops region, a few km S of Kanaka Bar by pullout on Hwy 1, 17 Aug 1995, *F. Lomer 95-166* (UBC); 8 km E of Kamloops, 26 May 1998, *P. Williston PW98-134* (UBC); W of Osoyoos, 1.3 km up Richter Mountain Road, 19 Jun 2006, *J.M. Saarela, C. Sears & J. Maze 628* (CAN, UBC).

15b. **Bromus squarrosus** L. var. **villosus** Roth, Neue Beytr. Bot. 1:109. 1802. (**Figs. 13C, 17**).

Similar to var. *squarrosus*, but glumes and lemmas densely pubescent with hairs to 0.8 mm long.

Distribution and Habitat — In North America *B. squarrosus* var. *villosus* is only known from the three southern British Columbia collections cited below. Additional occurrences in North America should be searched for in the field and in herbaria. Tzvelev (1976:335) indicated that, in its native range, the variety is somewhat rarer in distribution than the typical variety.

Notes.—Nomenclature used here follows Kerguélen (1999). *Bromus squarrosus* var. *villosus* Roth is reported here for the first time for continental North America. Material examined from British Columbia closely matches material seen from Russia [e.g., *Skvortsov s.n.* (CAN-578016!) collected in Volgograd]. The description for *B. squarrosus* by Pavlick (1995) and Pavlick & Anderton (2007) does not mention the presence of dense pubescence in the taxon, which suggests that these authors did not observe pubescent forms of the species. The 1993 record from British Columbia was collected by Pavlick, but this was likely long after he completed work on his revision of *Bromus* for North America (Pavlick 1995).

Specimens Examined. **CANADA. British Columbia:** Kootenay, Grand Forks, Gilpin Forest Service Road, E of Grand Forks, 23 Jun 1993, *L.E. Pavlick 93-143* (V); roadside pullout on W side of Hwy 1 (Trans Canada) at Hells Gate, 22 Jun 2006, *J.M. Saarela, C. Sears &*

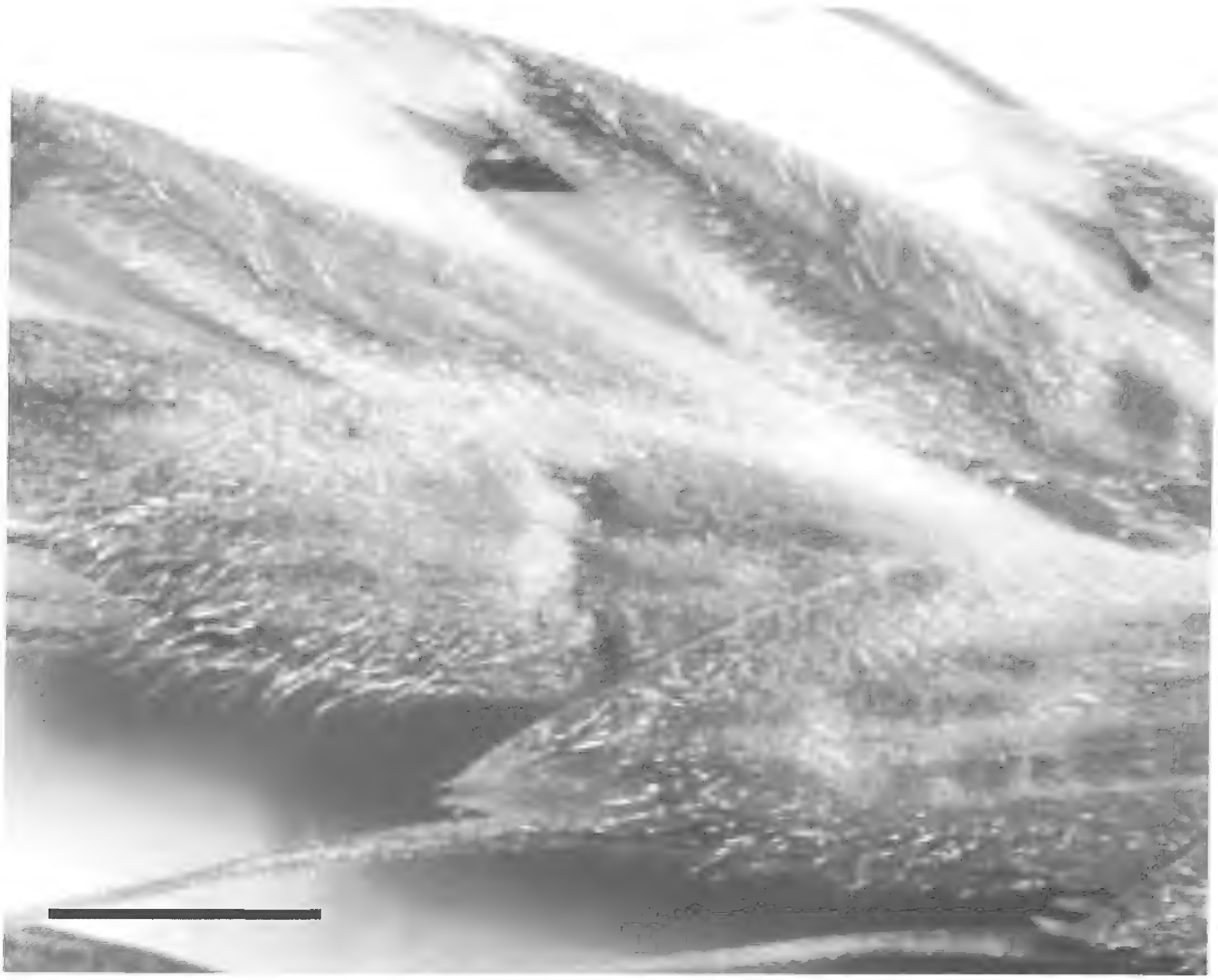

Fig. 17. Lemma morphology of *Bromus squarrosus* var. *villosus* [*Saarela, Sears & Maze 736* (CAN)], differing from the typical variety by the presence of dense pubescence to 0.8 mm long. Scale bar = 2.5 mm.

J. Maze 736 (CAN, UBC); Waneta, confluence of Columbia and Pend d'Oreille rivers, along railroad tracks opposite fishing pullover on Hwy 22A, 1400 ft, 17 Jun 2007, *F.L. Lomer 6268* (CAN, UBC, V).

16. Bromus sterilis L., Sp. Pl. 1:77. 1753. (**Figs. 18A–E, 19A**). *Schedonorus sterilis* (L.) Fr., Bot. Not. 131. 1843. *Genea sterilis* (L.) Dumort., Bull. Soc. Roy. Bot. Belgique 7:67. 1868. *Anisantha sterilis* (L.) Nevski, Trudy Sredne-Aziatsk. Gosud. Univ., Ser. 8b, Bot. 17:20. 1934. Type: ENGLAND. Surrey: Tothill, near Headley, scattered plants in derelict hay-field on heavy soil overlying chalk, 15 Jun 1932, *C. E. Hubbard 9045* (conserved type: E, proposed by Sales, Taxon 41:584. 1992; isoneotype: K).

Annual; rhizomes absent. Culms 25–110 cm tall, 2–4 mm wide at base, smooth; nodes 3–5, light to dark brown, glabrous, lower nodes usually covered by sheaths. Leaf sheaths closed for most of their length, open for 8–15 mm in length, moderately to densely pubescent with short stiff hairs to 0.5 mm; auricles absent; ligules 2.3–4.6 mm long, membranous, glabrous or pubescent, erose-lacerate; blades 4.5–22 cm long, 2–6 mm wide, adaxial surface glabrous, minutely pubescent or densely pilose with soft, wavy hairs to 2.5 mm long, long hairs sometimes only along the margins, abaxial surface minutely pubescent with small appressed hairs, margins smooth. Panicles 10–28 cm long, 3–18.5 cm wide, dense and ascending when young, becoming open and lax; branches usually longer than spikelets, shorter when panicle reduced to 1(2, 3) spikelets, 1(–3) spikelets per branch, lowest inflorescence node with 4–6 branches. Spikelets 4.5–6.7 cm long (including awns), cuneate, subcylindric-compressed, rachilla sometimes visible at maturity, florets 3–11.

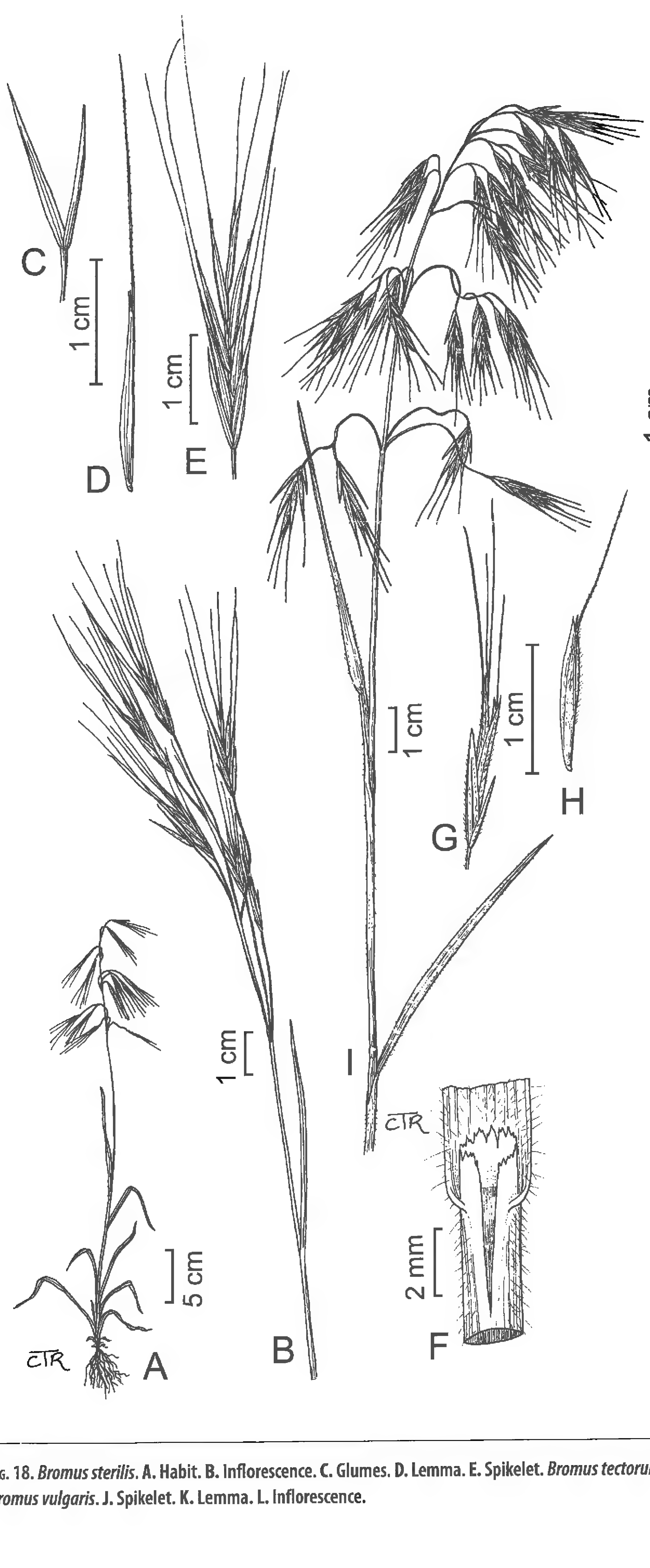

Fig. 18. *Bromus sterilis*. A. Habit. B. Inflorescence. C. Glumes. D. Lemma. E. Spikelet. *Bromus tectorum*. F. Ligule. G. Spikelet. H. Lemma. I. Inflorescence. *Bromus vulgaris*. J. Spikelet. K. Lemma. L. Inflorescence.

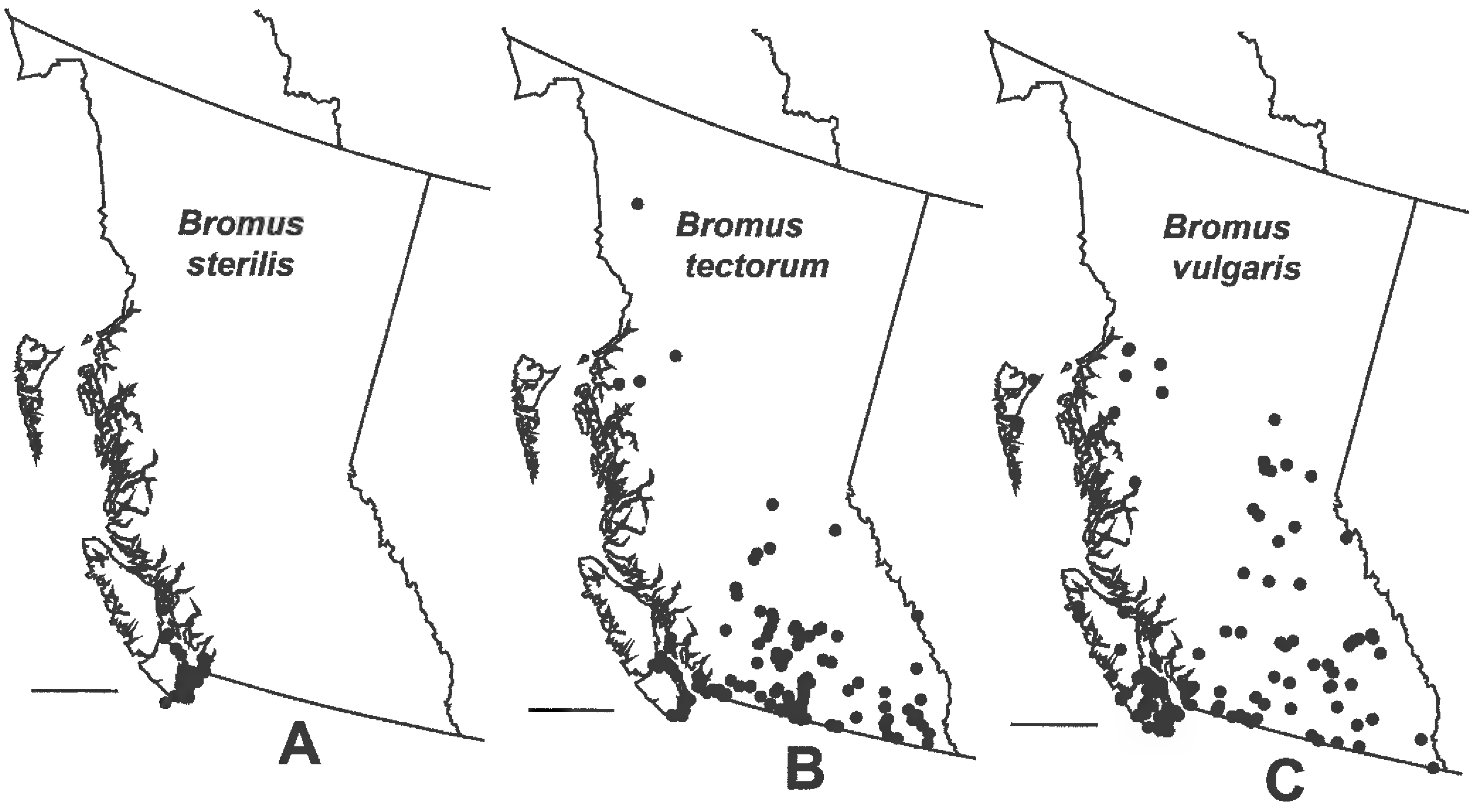

Fig. 19. Geographic distribution in British Columbia. A. *Bromus sterilis*. B. *Bromus tectorum*. C. *Bromus vulgaris*. Scale bars = 200 km.

Glumes subequal, lanceolate, smooth, keels smooth or scabrous, margins hyaline; lower glumes 10–14 mm long, 1–3-nerved; upper glumes 7.5–21 mm long, 3–5-nerved. Lemmas 13–22 mm long, 1.1–1.7 mm wide, 7-nerved, nerves conspicuous, lanceolate, backs smooth or scabridulous, scabrules sometimes increasing in density distally, margins not distinctly inrolled in fruit, apex bifid, the cleft 1–3 mm deep; awns 15–30 mm long, arising about 1.5 mm below lemma apex, straight, antrorsely scabrous. Paleas 9.5–13.5 mm long, much shorter than lemma, backs glabrous, keels glabrous or ciliate, cilia often present only distally, cilia to 0.2 mm long. Stamens 3; anthers 1.3–1.7 mm long, dark brown. $2n$ = 14, 28.

Distribution and Habitat.—Introduced. *Bromus sterilis* is native to Europe, northern Africa and south-western Asia (Sales 1993). In North America it occurs in western and eastern North America (Pavlick & Anderton 2007). In British Columbia *B. sterilis* occurs only in the extreme southwest of the province in the Vancouver area and on central to southern Vancouver Island (Fig. 19A). Habitats include roadsides, sandy beaches, meadows and waste places. Elevation: 0–425 m.

Common Names.—barren brome, poverty brome.

Notes.—Several intraspecific taxa that have been previously recognized are mentioned by Sales (1993:5-6), but she did not recognize these; none have been recognized in the North American flora.

Representative Specimens Examined. **CANADA. British Columbia:** vicinity of Victoria, 20 Jun 1908, *Macoun 76,833* (CAN); Victoria, Anderson's farm, 27 May 1893, *Macoun 117* (CAN); Victoria, 13 Jun 1908, *Macoun 76,835* (CAN); Vancouver Island, Saanichton, 15 May 1913, *Macoun 88,540* (CAN); Oak Bay, Victoria, 17 Jun 1913, *Macoun 88,541* (CAN, V); Victoria, 6 Jun 1908, *Macoun 76,834* (CAN); Victoria, 11 May 1920, *G.W. Copley 1-14* (DAO, UBC); Sidney, 30 Sep 1930, *H. Groh s.n.* (DAO); Shawnigan Lake, 27 May 1931, *H. Groh s.n.* (DAO); Crescent Beach, 31 May 1937, *J.W. Eastham s.n.* (CAN); Victoria, 2 Jun 1938, *J.W. Eastham 431* (DAO, UBC); W Point Grey, Jun 1939, *J.W. Eastham s.n.* (DAO); W Point Gray, Vancouver, Jun 1939, *J.W. Eastham 429* (UBC); Saanichton, 21 Jun 1939, *W.R. Foster s.n.* (DAO, UBC, V); James Island, off Saanichton, 5 Aug 1939, *H. Groh 424* (DAO); No. 5 road, Lulu Island, 0.25 mi S of Twigg Island, 4 Jun 1944, *J.W. Eastham 11426* (DAO, UBC); Whiffen Spit, Sooke, 19 May 1948, *V.C. Brink 48-28* (UBC); Victoria, Finlayson Point, 20 May 1950, 10 m, *V. Krajina & R.H. Spilsbury 3921* (DAO); Esquimalt Lagoon near Victoria, 7 May 1962, *J. Hett 90* (DAO); Happy Valley near Victoria, 30 May 1962, *J. Hett s.n.* (DAO); Henderson Point, Brentwood, 16 Jun 1967, *A. S. Harrison 20.1* (CAN); Victoria, Finlayson Point, 10 m, 20 May 1950, *V. Krajina & R.H. Spilsbury 3921* (UBC); 2 mi E of Duncan, 19 May 1955, *D.R. Lindsay & W. Woodbury 737* (DAO); John Dean Park, Saanichton, 14 Jun 1962, *J. Hett 16* (DAO); Little Saanich Mtn, 350 ft, 17 May 1965, *B.W. Davies 389* (DAO); Mt Finlayson, 425 m, 28 Jun 1978, *L. Pavlick 78-231* (V); Mt Finlayson, 300 m, 16 May 1979, 300 m, *L.E. Pavlick 79-6* (V); Saltspring Island, Mt Tuam, 3 Jul 1982, *L.E. Pavlick 82-19* (V); Vancouver Island, Mt Finlayson, E of Goldstream Provincial Park, 1 Jul 1982, *S.G. Aiken, S.J. Darbyshire & L.E. Pavlick 2118* (DAO); Mount Douglas Park, Saanich Peninsula, 4 Jul 1988, *S.J. Darbyshire 3792* (CAN, DAO); S end

of Tsawassen Drive S, Tsawassen Indian Reserve #0, 28 May 2006, *J.M. Saarela & C. Sears 546* (CAN, UBC); Mayne Island, Bennett Bay, Gulf Islands National Park Reserve of Canada, Wilkes Road off Bennett Bay Road, 3 Jun 2007, *J.M. Saarela, D.M. Percy & Y. Chang 826* (CAN, UBC); Mayne Island, cliff edge of Mount Park, ca. 1 km W of highest point where radar tower is, 3 Jun 2007, *J.M. Saarela, D.M. Percy, Y. Chang & Q. C. E. Cronk 808* (CAN, UBC); Vancouver Island, Thetis Lake Regional Park, just N of Hwy 1, N of Langford, 4 Jun 2007, *J.M. Saarela, D.M. Percy & Y. Chang 861* (CAN, UBC); Vancouver Island, just S of Chemanus along Hwy 1A, 6 Jun 2007, *J.M. Saarela, D.M. Percy & Y. Chang 909* (CAN, UBC); Vancouver Island, just off Hwy 19A along Crane Road, N of Qualicum Beach, at confluence of Nile Creek and the Straight of Georgia, 7 Jun 2007, *J.M. Saarela, D.M. Percy & Y. Chang 934b* (CAN, UBC).

17. Bromus tectorum L., Sp. Pl. 77. 1753. (**Figs. 18F–I, 19B**). *Zerna tectorum* (L.) Panz., Denkschr. Konigl. Akad. Wiss. Munchen 1813:297. 1814. *Schedonorus tectorum* (L.) Fries, Bot. Not. 131. 1843. *Anisantha tectorum* (L.) Nevski, Act. Univ. Asiae Med. 8b., Bot. 17:20, 22. 1934. *Genea tectorum* (L.) Dumort., Bull. Soc. Bot. Belg. 7:67. 1868., in adnot. Type: EUROPE: *Anon.* (Lectotype: LINN 93/25, designated by Smith, Notes. Roy. Bot. Gard. Edinb. 42:500. 1985).

Bromus tectorum var. *nudus* Klett & Richt., Fl. Leipzig 109. 1830. *Bromus tectorum* L. subsp. *nudus* (Klett & Richt.) Piper & Beattie, Fl. N. W. Coast 51. 1915. *Bromus tectorum* f. *nudus* (Klett & Richt.) St. John, Fl. S. E. Washington (Piper & Beattie) 36. 1937. *Bromus tectorum* f. *glabratus* (Spenn.) St. John, Fl. S.E. Washington (Piper & Beattie), ed. 2. 536. 1956. Type: not known.

Bromus setaceus Buckl., Acad. Nat. Sci. Phila. Proc. 1892:98. 1862. Type: U.S.A. Texas: *Buckley s.n.* (Lectotype: US-865474!, designated by Hitchcock, Man. Grass. U. S. 817. 1935).

Annual; rhizomes absent; 5–80 cm tall. Culms 0.7–2.5 mm wide at base, smooth; nodes 2–4, blackish brown, glabrous or minutely pubescent. Leaf sheaths closed for most of their length, glabrous or variously pubescent with dense, stiff hairs to 0.5 mm or long, soft, wavy hairs to 1 mm long, longer hairs to 2 mm long sometimes present towards sheath apex; auricles absent; ligules (1–)2–3 mm long, membranous, glabrous, erose-lacerate; blades 1.3–14 cm long, 1–5 mm wide, adaxial surface pubescent with sparse to dense short, stiff hairs to 0.3 mm long, abaxial surface puberulent with minute, appressed hairs ca. 0.1 mm long, hairs sometimes denser towards blade apex, margins smooth or with hairs like adaxial leaf surface. Panicles 4–22 cm long, 1–13.5 cm wide, condensed and ascending when young, becoming lax and nodding, sometimes reduced to a few spikelets, branches longer or shorter than spikelets, scabrous to densely pubescent, 1–14 spikelets per branch, lowest inflorescence node with 1–8 branches. Spikelets 2.5–3.5 cm long (including awns), cuneate, sometimes broadening at maturity, rachillaes sometimes visible at maturity; florets 3–6(–8). Glumes subequal, lanceolate, apices ± bifid, the cleft 0.1–0.5 mm deep, glabrous or minutely to densely pubescent with short, appressed hairs, with occasional long, soft hairs to 1 mm long, these sometimes occurring in a line just inside margins, margins hyaline, keels smooth or scabrous; lower glumes 4–9 mm long, 1(–3)-nerved, occasionally minutely awned, awn to 1.1 mm long; upper glumes 7–13.5 mm long, 3(–5)-nerved. Lemmas 9–13.8 mm long, (0.6–)0.9–1.5 mm wide, 7-nerved, backs glabrous, scabrous, or pubescent with long, soft hairs to 1 mm long, sometimes denser along margins and sometimes only pubescent on upper 2/3; keels smooth or serrulate, apex bifid, the cleft 1–3 mm deep; awns 8–18 mm long, arising 1.1–2.7 mm below lemma apex, straight, antrorsely scabrous. Paleas 7–8.7 mm long, shorter than lemma, backs glabrous and translucent, keels ciliate, cilia to 0.6 mm long. Stamens 3; anthers 0.5–0.9 mm long, dark brown. $2n = 14$.

Distribution and Habitat.—Introduced. *Bromus tectorum* is widespread across the United States and southern Canada, with scattered collections from locations in Alaska, Yukon and the western Northwest Territories (Pavlick & Anderton 2007; Valliant et al. 2007). The species is most common in the southern half of the province and it has been collected sporadically in northwestern British Columbia [Fig. 19B; see Valliant et al. (2007) for another recent distribution map]. Habitats include roadsides, fields, meadows, arid slopes, woodlands, cliffs and talus slopes, hillsides, dry rangeland, pastures, sandy beaches, railroad tracks and other waste places. Elevation: 0–1800 m.

Common Names.—English: cheatgrass, cheat grass, downy brome, drooping brome, early chess, military grass, thatch bromegrass; French: brome des toits, brome des murs.

Notes. —*Bromus tectorum* is a serious invasive weed. It was first recorded in North America from Pennsylvania in 1790, and the first report in western North America is from Spence's Bridge, British Columbia (Mack 1981; specimen cited below). Numerous genetic studies have indicated that *B. tectorum* in North America is highly inbreeding and has very low levels of genetic variation across its North American range (e.g., Novack et al.

1991; Bartlett et al. 2002; Ramakrishnan et al. 2006). Genetic variation within populations, however, shows strong regional differentiation, with populations in British Columbia having the highest level of within-population variation among those sampled across North America (Bartlett et al. 2002). Multiple introductions of *B. tectorum* into North America have been documented using genetic data (e.g., Mack 1981; Novack et al. 1991; Novack & Mack 1993, 2001; Bartlett et al. 2002). Valliant et al. (2007) provide an account of the introduction history of *B. tectorum* in British Columbia and Canada; based on allozyme data they identified a minimum of five independent introductions of *B. tectorum* into western Canada.

Representative Specimens Examined. **CANADA. British Columbia:** Spence's Bridge, 4 Jun 1889, *Macoun 29,989* (CAN); Mt Arrowsmith, 6 Aug 1900, *Fletcher and Anderson 22132* (DAO); Okanagan, Summerland, Jul 1912, *E. Wilson 1061* (UBC); Sidney, 7 Jul 1913, *M.O. Malte 27* (CAN); Spence's Bridge, 15 Jul 1913, *J. Davidson s.n.* (UBC); Twaal Valley, 21 Jun 1914, *J. Davidson s.n.* (UBC); near Moren's Ranch, Spence's Bridge, 21 Jun 1914, *J. Davidson s.n.* (UBC); Point Grey, 2 May 1915, *J. Davidson s.n.* (UBC); Pemberton Trail, 24 Jun 1916, *J.M. Macoun 93962* (CAN); Lillooet, 2 Jul 1916, *J.M. Macoun 93963* (CAN); Hazelton, Skeena River, 12 Jul 1917, *J.M. Macoun 93975* (CAN); Okanagan Lake, 17 Jun 1918, *A. H. Hutchinson s.n.* (UBC); Courtenay Lake, 21 Jun 1918, *Hutchinson s.n.* (UBC); Powell River, Jun 1923, *J. B. Munro s.n.* (UBC); White Rock, 25 May 1924, *T.R. Ashlee s.n.* (UBC); Eburne, 23 May 1931, *H. Groh s.n.* (DAO); Langley Prairie, 30 May 1931, *H. Groh s.n.* (DAO); Oliver, 3 Jun 1931, *H. Groh s.n.* (DAO); Kamloops, 4-7 Sep 1931, *V. Kujala & A. Cajander s.n.* (CAN); E of Lytton, 500 ft, 11 Jul 1932, *E.P. Hume s.n.* (UBC); near Kamloops, 2000 ft, 27 May 1934, *G. V. Copley 8* (DAO); near Cranbrook, 13 Aug 1934, *E.H. Moss 2942* (DAO); Spence's Bridge, Kamloops district, 24 May 1935, *D.W. Thompson s.n.* (DAO); Tranquille, Kamloops, Jun 1935, *E.W. Tisdale 40-11* (DAO); Lac du Bois, Tranquille, 21 Jul 1935, *E.W. Tisdale 40-11* (DAO); Squilax, 10 Aug 1935, *P.P. Henson s.n.* (DAO); Crescent Beach, 31 May 1937, *J.W. Eastham s.n.* (CAN); C. N. yards, Vancouver, 31 May 1937, *W. Sandall s.n.* (UBC); Nanaimo, 31 May 1939, *J.W. Eastham s.n.* (UBC); Kamloops, 14 Jun 1937, *J.H. Soper 1945* (DAO); Kamloops, 21 Jun 1937, *J.W. Eastham s.n.* (DAO); W Point Grey, Vancouver, 20 Jun 1937, *J.W. Eastham s.n.* (UBC); Marble Mts, Hat Creek Valley, 3000 ft, 26 Jun 1938, *J.W. Thompson & E. M. Thompson 227* (CAN, US); Lower Tranquille range, Kamloops, 22 May 1939, *E.W. Tisdale s.n.* (DAO); Prince Rupert-Terrace, Jul 1939, *C. C. King s.n.* (UBC); Terrace, 11 Aug 1939, *H. Groh 533* (DAO); Kamloops, 24 Jun 1940, *M.G. Dudley 246* (DAO); Locarno Park, Vancouver, 11 Jun 1944, *J.W. Eastham s.n.* (UBC); Gray Creek, 1 Jul 1944, *W.C. McCalla 8351* (UBC); Fort Steele, 12 Jul 1944, *W.B. Johnstone 495* (UBC); Kimberley, *F. Fodor 28*, 14 Jul 1946 (UBC); Osoyoos, 3 Jul 1947, *V.C. Brink s.n.* (UBC); Lytton, 175-500 m, 18 Aug 1949, *V.J. Krajina 1207* (UBC); Anarchist Mt, 19 Aug 1950, *V.J. Krajina s.n.* (UBC); Princeton, 19 Aug 1950, *V.J. Krajina s.n.* (UBC); Coyle, Merritt, 28 Aug 1950, *V. Krajina s.n.* (UBC); Chase, Kamloops, 28 Aug 1950, *V.J. Krajina s.n.* (UBC); 1 mi S of Osoyoos on W side of lake, 19 May 1953, *J.A. Calder & D.B.O. Savile 7899* (DAO); 10 mi SE of Hedley along Similkameen River, 26 May 1953, *J.A. Calder & D.B.O. Savile 8226* (DAO); along Nicola River about 5 mi SW of Spence's Bridge, 31 May 1953, *J.A. Calder & D.B.O. Savile 8457* (DAO); about 4 mi E of Kamloops on N side of S Thompson River, 2 Jun 1953, *J.A. Calder & D.B.O. Savile 8590* (DAO); about 4 mi S of Sicamous on E side of Mara Lake, 5 Jun 1953. *J.A. Calder & D.B.O. Savile 8749* (DAO); Westbank, 8 Jun 1953, *n.c.* (DAO); 24 mi S of Kootenay Bay along highway to Creston, 12 Jun 1953, *J.A. Calder & D.B.O. Savile 9047* (DAO); Goat River canyon at Erickson near Creston, 17 Jun 1953, *J.A. Calder & D.B.O. Savile 9285* (DAO, US); 2.5 mi E of Castlegar on highway between Nelson and Rossland, 20 Jun 1953, *J.A. Calder & D.B.O. Savile 9428* (DAO, UBC); Christina Lake, 29 Jun 1953, *G.H. Collin s.n.* (DAO); Westbank, 8 Jul 1953, *J.M. Smith s.n.* (DAO); Invermere townsite, 14 Jul 1954, *A. McLean s.n.* (DAO); Parksville, Vancouver Island, May 1955, *V.C. Brink s.n.* (DAO, UBC); Osoyoos, 12 May 1955, *D.R. Lindsay & W. Woodbury 595* (DAO); near Bowser, Qualicum Bay, Vancouver Island, 16 May 1955, *D.R. Lindsay & W. Woodbury 637* (DAO); Port Alberni, 17 May 1955, *D.R. Lindsay & W. Woodbury 660* (DAO); 20 mi N of Victoria, 19 May 1955, *D.R. Lindsay & W. Woodbury 725* (DAO); Patricia Bay Highway, one-half mi N of Royal Oak Corner, 20 May 1955, *D.R. Lindasy & W. Woodbury 753* (DAO); S of Steveston, Lulu Island, 24 May 1955, *D.R. Lindsay & W. Woodbury 770* (DAO); Abbotsford, 25 May 1955, *D.R. Lindsay & W. Woodbury 795* (DAO); Boston Bar, 30 May 1955, *D.R. Lindsay & W. Woodbury 861* (DAO); 4 mi S of Spence's Bridge, 31 May 1955, *D.R. Lindsay and W. Woodbury 884* (DAO); 5 mi N of Kamloops, 1 Jun 1955, *D.R. Lindsay & W. Woodbury 897* (DAO); 10 mi N of Merritt, Nicola Valley, 2 Jun 1955, *D.R. Lindsay & W. Woodbury 906* (DAO); Williams Lake, 5 Jun 1955, *D.R. Lindsay & W. Woodbury 971* (DAO); near Pavilion, 7 Jun 1955, *D.R. Lindsay & W. Woodbury 995* (DAO); 2 mi N of Vernon, 10 Jun 1955, *D.R. Lindsay & W. Woodbury 1023* (DAO); Lumby, 14 Jun 1955, *D.R. Lindsay & W. Woodbury 1073* (DAO); 10 mi S of Vernon, 15 Jun 1955, *D.R. Lindsay & W. Woodbury 1096* (DAO); 31 mi S of Williams Lake, 22 Jul 1955, *G.A. Mulligan & W. Woodbury 1762* (DAO); Fairview on Okanagan Falls to Oliver Rd, via Green Lake, 1650 ft, 11 May 1958, *K. Beamish 8161* (DAO); between Lytton and Lillooet, 4 Aug 1958, *T.M.C. Taylor, V. Krajina & F. Tusko 2* (UBC); Cranbrook, 12 Jul 1959, *E.W. Sullivan 559430* (DAO); Kaslo, Kootenay, 2200 ft, 21 Aug 1959, *M. Bell s.n.* (UBC); Indian Reserve E of Oliver, 4 May 1960, 1600 ft, *K. Beamish & E. Vrugtman 60102* (CAN); Indian Reserve E of Oliver, 4 May 1960, *J.W. Eastham 60102* (US); between Windermere and Fairmont Hotsprings, ca. 3000 ft, 13 May 1960, *K. Beamish & F. Vrugtman 60318* (UBC); Oliver campsite, 1100 ft, 17 May 1960, *K. Beamish & F. Vrugtman 60423* (UBC); Boy's Town, Hope-Princeton Hwy, 2300 ft, 11 Jul 1960, *K.I. Beamish & F. Vrugtman 60648* (DAO); Mt Kobau lookout trail, S Okanagan, 3500 ft, 8 Jul 1961, *J.W. Eastham 610412* (CAN, UBC); Esquimalt Lagoon, near Victoria, 7 May 1962, *J. Hett s.n.* (DAO); coast of Saanich Peninsula near Victoria, 11 May 1962, *J. Hett s.n.* (DAO); Esquimalt Lagoon Near Victoria, 29 May 1962, *J. Hett s.n.* (DAO); Manning Provincial Park, about 30 mi. SW of Princeton and 90 mi E of Vancouver, 4000-5000 ft, 26 Jun 1964, *H.J. Scoggan 15093* (CAN); Okanagan Range between Princeton and Penticton, 26 Jun 1964, *H.J. Scoggan 15044* (CAN); Nanoose Bay, 10 ft, 6 May 1965, *B.W. Davies 256* (DAO); Little Saanich Mtn, 400 ft, 17 May 1965, *B.W. Davies 390* (DAO); Esquimalt Lagoon, 1 Jun 1965, *B.W. Davies & R.A. Keller 700* (DAO); S of Kamloops, between Shumway and Trapp Lakes, 2300 ft, 23 Jun 1965, *V.J. Krajina*

(DAO); NW slopes above E end of Nicola Lake, 40 mi. S of Kamloops, 1900 ft, 23 Jun 1965, *V.J. Krajina 650623139* (UBC); 34 mi N of Princeton, 23 Jun 1965, *V.J. Krajina 650623192* (UBC); Beaver Pond, Manning Park, 14 Jul 1965, *I. L. Bayly 65-129* (DAO); S of Kamloops, 2830 ft, April 1966, *V.J. Krajina 65062303* (CAN, UBC); Island View Beach, Vancouver Island, 25 ft (7.6 m), 25 May 1966, *A.S. Harrison 29.1* (CAN); 2 mi N of Princeton, 2300 ft, 31 May 1966, *J. F. Alex 2258* (DAO); Aspen Grove, on W shore of Kidd Lake, along Hwy no. 5, 3000 ft, 22 Aug 1969, *J.H. Soper, M.J. Shchepanek & A.F. Szczawinski 12,662* (CAN); S Kelowna, 14 Jun 1970, *S. Kojima s.n.* (UBC); Manning Park, along Hope-Princeton Hwy, Beaver Pond area, 1189 m (3900 ft), 22 Jun 1973, *C.C. Chuang 118* (CAN); between Deese Lake and Telegraph Creek, 17 Jul 1973, *V.J. Krajina, R.G. McMinn, K. Klinka & R. M. Annas s.n.* (UBC); Botanie Valley road near Lytton, 1200 ft, 18 May 1974, *J. Pinder-Moss & J. Pojar 657* (UBC); Nanoose Hill, E side of Nanoose Bay, ca. 15 mi N of Nanaimo, Vancouver Island, < 500 ft, 27 May 1975, *K.I. Beamish, E. Perkins & S. Campbell 750045* (DAO); Ashnola Road, mile 23, 24 Jul 1975, *R. Hainault 7639* (DAO); Cathedral Park, 2 Jul 1976, *R. Hainault 7766* (DAO, UBC); Quesnel Region, S of Quesnel on Hwy 97, 16 Jul 1976, *M. Barkworth 1640* (DAO); Okanagan Game Farm, 1 mi NE of Kaleden, 1800 ft, 23 May 1977, *B. Wikeem & S. Gale s.n.* (UBC); W of Prentice Lake trail and N of Relay Creek, 1800 m, 16 Jun 1977, *C. Selby 20* (DAO, UBC); Hat Creek valley, 3300 ft, 23 Jun 1977, *R.K. Scagel 77-0-83* (UBC); above trail to Prentice Lake, plot 134 #880, 1580 m, 8 Aug 1977, *C. Selby s.n.* (DAO); Nanoose Hill, N of Nanaimo, 2-4 May 1980, *R. Turkington s.n.* (UBC); Kamloops, Lac du Bois Range behind Research Station, 23 Jun 1980, *S.G. Aiken 1062* (DAO); Kamloops Road to Todd Mt, 2800 ft, 30 Jun 1980, *S.G. Aiken 1118* (DAO); Opax Mountain, near Kamloops, 1 Jul 1980, *S.G. Aiken 1130* (DAO); Prison Camp, 20 km N of Clearwater Village, 8 Sep 1980, *T. Goward 81-815* (DAO); E of Princeton on Hwy 3 along Similkameen River, 31 Jul 1980, *H.L. Dickson & M. Picher 3757* (DAO); Kent District, Harrison Lake, Harrison Hot Springs, 10 Jul 1982, *S.G. Aiken & S.J. Darbyshire 2237* (DAO); Kalamalka Lake Park, near Vernon, 23 May 1984, *A. Ceska and R.T. Ogilvie 17659* (UBC); Meager Creek Hot Springs, N of Pemberton, Lillooet District, 650 m, 9 May 1987, *A.A. Rose s.n.* (UBC); below "The Throne", adjacent to the Haines Lease Ecological Reserve, N of Osoyoos Lake, 19 May 1987, *W.J. Crins & S.G. Cannings 7380* (UBC); Summerland, 30 Jun 1988, *J. E. Whiting 36* (UBC); Osoyoos area, Haynes Lease Ecoreserve, 13 May 1990, *T. Goward & T. Lea 90-593* (UBC); Christina Lake, 28 Aug 1990, *D.M. Tiedje 5581* (DAO); Abbotsford Distr. Munic., near base of Sumas Mt, 60-80 m, 25 May 1995, *H. Kennedy, F.R. Ganders, M. Marshall, D. Justice & L.Goertzen 4849* (UBC); 1.9 km up Kruger Mountain Road, S of Old Richter Pass Road, W of Osoyoos, 26 May 1995, *H.L. Dickson 8719* (DAO); Hope, above Fraser River, ca. 200 m., 1 Jun 1995, *H. Kennedy, F.R. Ganders & L. Thacker 4892* (UBC); Texada Island, off Harwood Point, at SE end of Dick Island, 2–5 m, 19 Jun 1997, *H. Janszen, P. Janszen & M. Fontaine 2659B* (UBC); 8 km E of Kamloops, 600 m, 11 Jun 1998, *P. Williston s.n.* (UBC); 12 km SW of Merritt, 27 Jul 1998, *P. Williston PW98-400a* (UBC); W perimeter of middle field on Basque Ranch (IR 18), 14 May 1999, *R. Bandringa 89* (UBC); Kootenay, Grand Forks, 30 Aug 1999, *R. Hebda s.n.* (UBC); edge of beach above wrack line, below University of British Columbia, 25 May 2005, *J.M. Saarela 316* (CAN, UBC); along Hwy 3, E of Hedly, 2.5 km W of Keremeos, gravel picnic area (rest stop), 18 May 2006, *J.M. Saarela 336* (CAN, UBC); Rocky Mountain Forest District, along Hwy 3, 1.5 km E of Elko, 23 May 2006, *J.M. Saarela 404* (CAN, UBC); Fort Steele Road, corner of Hwy 3 and Wardner, 12 km W of Jaffray, 23 May 2006, *J.M. Saarela 413* (CAN, UBC); Rampart Rest Area, 10 km E of Cranbrook, 23 May 2006, *J.M. Saarela 416* (CAN, UBC); ca. 2 km E of Erickson along Hwy 3, 24 May 2006, *J.M. Saarela 440* (CAN, UBC); 21.1 km W of Creston on Hwy 3A, 24 May 2006, *J.M. Saarela 446* (CAN, UBC); Kuskanook Rest Area, Kuskanook Harbour Society, 24 May 2006, *J.M. Saarela 450, 451* (CAN, UBC); Shady Lake Campground, 4.7 km S of Osoyoos at U.S.A./ Canada border, 25 May 2006, *J.M. Saarela 471* (CAN, UBC); Osoyoos, Haynes Provincial Park, 25 May 2006, *J.M. Saarela 485* (CAN, UBC); Richmond, London Farm, Gilbert Beach, just E of London's Landing, 28 May 2006, *J.M. Saarela & C. Sears 525* (CAN, UBC); Ladner, S side of Canoe Passage, W terminus of River Road, 28 May 2006, *J.M. Saarela & C. Sears 539* (CAN, UBC); 10 km W of Princeton on Hwy 3, 19 Jun 2006, *J.M. Saarela, C. Sears & J. Maze 587* (CAN, UBC); Princeton, across from Princeton High School, 19 Jun 2006, *J.M. Saarela, C. Sears & J. Maze 596* (CAN, UBC); N of Princeton, ca. 6 km along Iron Mountain Road, beyond 2nd fence, 19 Jun 2006, *J.M. Saarela, C. Sears & J. Maze 603* (CAN, UBC); 1.9 km up Stemwinder Mountain Road, 19 Jun 2006, *J.M. Saarela, C. Sears & J. Maze 608* (CAN, UBC); Fairview Road, ca. 4 km NE from intersection with Lowe Road, 19 Jun 2006, *J.M. Saarela, C. Sears & J. Maze 622* (CAN, UBC); University of British Columbia, beside Biological Sciences Building, 8 Sep 2006, *J.M. Saarela 761* (CAN).

18. Bromus vulgaris (Hook.) Shear, Bull. Div. Agrostol., U.S.D.A. 23:43, f. 24. 1900. **(Figs. 18J-L, 19C).**

Bromus purgans var. *vulgaris* Hook., Fl. Bor.-Amer. 2:252. 1840. *Bromus eximius* subsp. *umbraticus* Piper, Contr. U. S. Natl. Herb. 11:144. 1906, nom. illeg. superfl. *Bromopsis vulgaris* (Hook.) Holub, Folia Geobot. Phytotax. 8:169. 1973. *Zerna vulgaris* (Hook.) Henrard, Blumea 4:498. 1941. Type: U.S.A.: Columbia River, *Scouler s.n.* (lectotype: K, designated by Wagnon, Brittonia 7:459. 1952; isotype: US–A865457!, fragment ex. K).

Note: Hooker (1840:252) cited four collections when he described *B. purgans* var. *vulgaris*: "*Goldie. Dr Richardson.* Red River. *Douglas.* Columbia. *Dr Scouler*," and he cited "Fort Norman. *Dr Richardson*" following a description for a subvariety. Shear (1900) was the first to recognize *B. vulgaris* at the species level. He indicated that a spikelet from the Scouler specimen matched those of other taxa that he included as synonyms of *B. vulgaris* (i.e., *B. ciliatus* var. *pauciflorus* Vasey in Beal and *B. debilis* Nutt. ex Shear). Piper (1906) created a new name (*Bromus eximius* var. *umbraticus* Piper) for Shear's taxon, indicating that it is not the same as *B. purgans* var. *vulgaris* Hook., seemingly unaware that some of the material that Hooker examined is indeed *B. vulgaris* in the sense of Shear (1900). Wagnon (1952) recognized *B. vulgaris* Shear and placed Piper's new name for this taxon into its synonymy. Wagnon (1952) indicated that he observed all of Hooker's original material at Kew except "*Goldie. Dr. Richardson.*" He noted that the Douglas collection (two specimens) from "Red River" is *B. kalmii* Gray; Richardson's "Fort Norman" collection is *B. inermis* var. *purparascens* (=*B. inermis* Leyss.); and Dr. Scouler's collection from "Columbia [River]" is *B. vulgaris*, in the sense of the taxon according to Shear (1900), who saw a spikelet

from the same collection. This concept of *B. vulgaris* has been taken up by all subsequent authors. Wagnon (1952) further noted that Richardson and Goldie collected (independently) east of the Rocky Mountains, outside the range of *B. vulgaris*, and suggested (reasonably) that their collections are likely different *Bromus* taxa. Wagnon (Brittonia 7:459. 1952) designated the Scouler collection as the type [lectotype] of *B. purgans* var. *vulgaris*, making *B. eximius* var. *umbraticus* a superfluous illegitimate name. His choice of this specimen as lectotype is not in conflict with the original protologue for the name, since the brief description given is not sufficiently detailed to distinguish among the mixed taxa that Hooker examined. Pavlick et al. (2003) erroneously indicated that the correct name for *B. vulgaris* (Hook.) Shear is *B. eximius* subsp. *umbraticus* Piper, and did not indicate that Wagnon (1952) lectotypified *B. purgans* var. *vulgaris*, since they listed Hooker's original material as syntypes and included the independent collections of Goldie and Richardson as a single collection.

Bromus vulgaris var. *eximius* Shear, Bull. Div. Agrostol., U.S.D.A. 23:44. 1900. *Bromus eximius* (Shear) Piper, Contr. U.S. Natl. Herb. 11:143. 1906. Type: U.S.A. Oregon. Wallowa Co.: on moist, open mountain side 4 mi above Wallowa Lake, 23 Aug 1899, *C.L. Shear 1791* (holotype: US-81575!).

Bromus vulgaris var. *robustus* Shear, Bull. Div. Agrostol., U.S.D.A. 23:44. 1900. *Bromus eximius* var. *robustus* (Shear) Piper, Contr. U.S. Natl. Herb. 1:143. 1906. Type: U.S.A. Oregon. Clatsop Co.: in moist thickets near the seashore, Seaside, 11 Aug 1899, *C.L. Shear & F.L. Scribner 1710* (isotype: US-81576!).

Bromus ciliatus var. *glaberrimus* Suksd., Deutsche Bot. Monatsschr. 19:93. 1901. Type: U.S.A. Washington. Skamania Co.: 22 Jul 1894, *W.N. Suksdorf 2335* (isotypes: GH–234940, US–228545! with the additional locality information: "near the Ice Cave").

Perennial; rhizomes absent; plants 45–125 cm tall. Culms 2–5(–9) mm wide at base, smooth; nodes (3–)4–6(–7), brown, glabrous or finely to densely retrorsely pubescent, hairs to 0.7(–1) mm long, occasionally with denser hairs above nodes; lower nodes covered by sheaths. Leaf sheaths closed for most of their length, glabrous or sparsely to densely pilose with hairs to 1.2 mm long; auricles absent; ligules (2–)3–6(–7) mm long, membranous, glabrous, erose; blades 12–33 cm long, 3–16 mm wide, thin and papery when dry, adaxial surface sparsely to densely pilose, hairs to 1 mm long, soft and wavy, abaxial surface glabrous, margins smooth or serrulate. Panicles 8–25 cm long, 1–5 cm wide, narrow, branches erect to ascending or drooping, shorter or longer than spikelets, branches scabrous-pubescent, 1(–2) spikelets per branch, lowest inflorescence node with 1–5 branches. Spikelets 1.5–3 cm long, ovate-lanceolate, terete to slightly compressed, rachilla sometimes visible at maturity; florets 3–9. Glumes subequal, lanceolate, glabrous or pubescent, hairs sometimes restricted to margins and keel; lower glumes 4–9 mm long, 1(–3)-nerved, lanceolate; upper glumes 5–11 mm long, 3-nerved, sometimes mucronate, mucros to 0.5 mm long. Lemmas 10–16 mm long, 7-nerved, 1.2–2 mm wide, margins glabrous to sparsely or densely pubescent, backs glabrous to variously pubescent, hairs to 1 mm long, sometimes denser on lower ½; apex entire or minutely bifid, the cleft to 0.3 mm deep; awns (4–)6–11 mm long, arising 0–0.5 mm below lemma apex, straight, antrorsely scabrous. Paleas 7.5–11 m long, shorter than lemmas, keels densely ciliate, cilia to 0.5 mm long. Stamens 3; anthers 2–3.5(–4) mm long, dark brown. $2n = 14$.

Distribution and Habitat.—Native. In North America, *B. vulgaris* occurs in British Columbia, southwestern Alberta and south to western Wyoming and south–central California (Pavlick & Anderton 2007). *Bromus vulgaris* occurs throughout the southern half of British Columbia (Fig. 19C). It was only recently reported from Moresby Island (Queen Charlotte Islands; Lomer & Douglas 1999). A 2007 collection [*Saarela & Percy 1169* (CAN, UBC)] represents the first record of *B. vulgaris* from the neighbouring Graham Island. Habitats include moist woods, stream banks, damp thickets, along trails, meadows and rocky banks. Elevation 0–2286 m.

Common Names.—Columbia brome, narrow-flowered brome, common brome.

Notes.—In herbarium material of *B. vulgaris*, leaf blades tend to appear conspicuously thin and papery compared to those in other species of *B.* sect. *Bromopsis*, though it is difficult to adequately describe this qualitative characteristic. This characteristic does not seem to be as evident in the field. At present, there are no leaf blade anatomical data for North American *B.* sect. *Bromopsis* species which might allow further evaluation of this character.

Representative Specimens Examined. **CANADA. British Columbia:** Selkirk Range, 17 Aug 1885, *Macoun 30,005* (CAN); Roger's Pass, Selkirk Mtns, 18 Aug 1885, *J. Macoun 30005*; Nanaimo, 7 Jun 1887, *J. Macoun s.n.* (US); Goldstream, Vancouver Island, 5 Jul 1887, *Macoun 30009* (CAN); Goldstream, Vancouver Island, 5 Jul 1887, *Macoun 30,010* (CAN, US); Deer Park, Lower Arrow Lake, 18 Jun 1890, *Macoun 30014* (CAN, US); Middle Selkirk Mts, Rogers Pass, 4500 ft, 1 Aug 1890, *Macoun 11084* (CAN, US); Selkirk Mts, Rogers Pass, 4 Aug 1890, *Macoun 30007* (CAN); Nanaimo, Vancouver Island, 14 Jul 1893, *Macoun 135* (CAN); Cameron Lake, Vancouver Island, Jul-Aug 1899,

Fletcher 2213.5 (DAO); Chilliwack River, 19 Jun 1901, *J.M. Macoun 26060* (CAN, US); Chilliwack Valley, 21 Jun 1901, 1800 ft, *J.M. Macoun 26063* (US); Chilliwack Lake, 2500 ft, 22 Jul 1901, *J.M. Macoun 26062* (CAN, US); Chilliwack River, 2 Aug 1901, *J.M. Macoun 26064* (CAN, US); Chilliwack River, 8 Aug 1901, 2000 ft, *J.M. Macoun 26061* (CAN, US); Vancouver Island, 31 Jul 1902, *C.O Rosendahl 856* (US); Vancouver, 22 Jul 1902, *C.O. Rosendahl 802* (US); Skagit Valley, 24 Jun 1905, *J.M. Macoun 72949* (CAN, US); Glacier, Illecillewaet Valley, Loop Trail, 3500–4000 ft, 20 Jul 1906, *S. Brown 656* (CAN); vicinity of Victoria, 18 Jun 1908, *J. Macoun 78833* (US); head of Departure Bay, 23 Jun 1908, *J. Macoun 76,848* (US); Departure Bay, near Biological Station, 3 Jul 1908, *Macoun 76846* (CAN, US); Mt Benson near Nanaimo, 13 Jul 1908, *J. Macoun s.n.* (US); vicinity of Victoria, 20 Jul 1908, *J. Macoun 76845* (US); Colquitz River near Victoria, 20 Jul 1908, *Macoun 76,850* (CAN, US); S shore of Cowichan Lake, 15 Jun 1909, *C.O. Rosendahl 1819* (US); Bear Lake, 3 Jul 1911, *W. Spreadborough 87613* (US); Bear Lake, 5 Jul 1911, *W. Spreadborough 87601* (US); Eburne, 3 Jun 1912, *J. Davidson s.n.*(UBC); Sidney, 7 Jul 1913, *M.O. Malte 28* (CAN); vicinity of Sidney, 12 Jun 1913, *J. Macoun s.n.* (V); Mayne Island, 4 Jun 1914, *J.M. Macoun 90083* (CAN); Oak Bay, near Victoria, 17 Jun 1913, *J. Macoun 88,528* (CAN); Vancouver Island, Alberni, Jun 1916, *W.R. Carter 906* (CAN); Cascade Range, near head of McGillivray Creek, 5000 ft, 10 Aug 1916, *J.M. Macoun 94,020* (CAN, US); Cascade Range, within five miles of Lillooet, 22 Jul 1916, 3000 ft, *J.M. Macoun 93,966* (CAN); Cascade Range, within five mi of Lillooet, 2500 ft, 22 Jul 1916, *J.M. Macoun 93,970* (CAN); Cascade Range, near head of McGillivray Creek, 5000 ft, 12 Aug 1916, *J.M. Macoun 93,976* (CAN); Kootenay, Crawford Bay, 20 Jun 1918, *J.W. Kidman s.n.* (UBC); Sidney, 4 Jul 1921, *M.O. Malte 106,800* (CAN, DAO); Vancouver Island, Cowichan Lake, 25-26 Aug 1931, *V. Kujala and A. Cajander s.n.* (CAN); Vancouver Island, Victoria, Goldstream, 11-12 Sep 1931, *V. Kujala & A. Cajander s.n.* (CAN); Tabor Lake (Six-mile Lake), 6 mi E of Prince George, 14-18 Jul 1931, *V. Kujala & A. Cajander s.n.* (CAN); Mt between Chilliwack and Hope, 3000 ft, 9 Jul 1932, *E. P. Hume s.n.* (UBC); Athabasca Mill, Nelson, 4000 ft, 16 Jul 1937, *J.W. Eastham 403* (UBC); Venus Mine, Nelson, 5000 ft, 18 Jul 1937, *J.W. Eastham 404c* (UBC); Hollyburn Trail, 1 Jul 1938, *J.W. Eastham 406a* (UBC); Beacon Hill Park, Victoria, 2 Jun 1938, *J.W. Eastham 849* (UBC); Rossland Highway, Grand Forks, 18 Jul 1938, *J.W. Eastham s.n.* (DAO, UBC); Victoria, 11 Jun 1939, *J.W. Eastham s.n.* (DAO); Qualicum Falls Park, Vancouver Island, 31 Jun 1939, *J.W. Eastham 401* (UBC); Mt Revelstoke, 3000 ft, 18 Jul 1939, *H. Groh 186* (DAO); Goldstream Lake, Vancouver Island, 13 Jun 1940, *I. Cowan 8156* (UBC); Mavis Lake, Vancouver Island, 13 Jun 1940, *I. Cowan 8166* (UBC); Long Beach, Nelson, 17 Jun 1940, *J.W. Eastham 7384* (UBC); Nelson, 25 Jun 1940, *J.W. Eastham 7540* (UBC); Lightning Peak Road, Monashee, 5000 ft, 14 Jul 1940, *J.W. Eastham 7851* (UBC); Parksville, Vancouver Island, 10 Jun 1941, *J.W. Eastham 8887* (UBC); Cultus Lake, Chilliwack, 11 Jun 1941, *J.W. Eastham 8897* (UBC, US); Seymour Park, N shore, 21 Jun 1941, *J.W. Eastham 8953* (UBC, US); Alberni, Vancouver Island, 10 Aug 1941, *J.H. Soper 8378* (DAO); Arrowsmith Trail, Cameron Lake, 14 Aug 1941, *J.W. Eastham 9436* (UBC); W Vancouver, 15th Street, 20 Jun 1943, *J.W. Eastham 10834a* (UBC); Manning Park, 4000 ft, 25 Jul 1945, *G.A. Hardy 14240* (UBC); Aleza Lake, 23 Jul 1946, *J.W. Eastham 14809* (UBC); Vancouver, 120 ft, 19 Jul 1949, *V. Krajina 74* (UBC); Botanic Valley, 22 Aug 1949, *V.J. Krajina s.n.* (UBC); Salmon River Valley 15 mi S of Sayward, 65 m, 3 Jun 1950, *V. Krajina & R.H. Spilsbury 4302* (UBC); Qualicum Beach, 25 Jun 1950, 10 m, *V. Krajina, R.H. Spilsbury & A. Szczawinski 4591* (DAO, UBC); Vancouver Island, Wolf Mountain, 300 m, 27 Jul 1950, *V. Krajina, R.H. Spilsbury, & A. Szczawinski 5171* (UBC); MacMillan Park, 185 m, 8 Aug 1950, *V. Krajina, R.H. Spilsbury & A. Szczawinski 5331* (UBC); Goodchap Mt, E of Apex Mt near Penticton, 5-7500 ft, 27 Jul 1950, *D. Martin s.n.* (UBC); 0.5 mi W of 2nd Lake, 29 Jul 1950, *V. Krajina, R.H. Spilsbury & A. Szczawinski 5195* (DAO); Vancouver Island, MacMillan Park, 185 m, 8 Aug 1950, *V. Krajina, R.H. Spilsbury & A. Szczawinski 5329* (UBC); under Monashee Pass, 10 Jul 1952, *V.J. Krajina s.n.* (UBC); middle Nanaimo River Valley, 700 ft, 16 Jun 1955, *D. Mueller-Dombois 22-8* (UBC); Ganges, 30 Jun 1956, *T.R. Ashlee 36* (UBC); Nanaimo River Valley, 700 ft, 11 Jul 1955, *D. Mueller-Dombois 40-1* (UBC); Boundary Creek 10 mi N of Greenwood, 30 Jul 1956, *A. McLean s.n.* (DAO); W Nanaimo River Valley, 1115 ft, 6 Aug 1957, *D. Mueller-Dombois 18-1* (UBC); 9.5 mi on road from Beaver Lake to Likely, NW of Williams Lake, 28 Aug 1956, *J.A. Calder, J.A. Parmelee & R.L. Taylor 20505* (DAO); Du Hamel Lakes, Nelson, Kootenay, 26 Jul 1958, *M. Bell s.n.* (UBC); Sugar Lake, Cherryville, 28 Jun 1958, *M. Bell s.n.* (UBC); Big Qualicum River, Vancouver Island, 13 Jul 1959, *L. Holm 524* (UBC); Nakusp, Kootenay, 2400 ft, 22 Jul 1959, *M. Bell s.n.* (UBC); E side of Lightning Lake, Manning Park, 4000 ft, 13 Jul 1960, *K.I. Beamish & F. Vrugtman 60756* (DAO, UBC); Head of Finlayson Arm, N of Victoria, 16 Jul 1961, *J.A. Calder & K.T. Mackay 31521* (DAO); Gail Falls on Kelsey Bay-Campbell River road, 12 Aug 1961, *J.A. Calder & K.T. MacKay 32432* (DAO); Sarita River, 50 ft, 14 Jun 1963, *A. Yound & W. Hubbard 395* (DAO); 1 mi E of Pilot Mountain Lookout, ca. 15 mi NE of Prince George, 1 Jul 1963, *A. Auclair 15* (DAO); Kennedy River area, drainage of Kennedy River, 2 Jul 1963, *A. Young & W. Hubbard 226* (DAO); Pilot Mountain Road, 1 mi E of the lookout, 2000 to 2400 ft, 2 Jul 1963, *A. Auclair & S. Eis s.n.* (DAO); Lawless Creed Road, 13.6 mi W of Tulameen, NW of Princeton, 4500 ft, 16 Jul 1964, *A. McLean s.n.* (DAO); Mt Revelstoke National Park, 2040 ft, 22 Jun 1965, *V.J. Krajina 65062233* (UBC); Copper Mtn Road, 2.7 mi S of rock cut, S of Princeton, 5800 ft, 6 Aug 1964, *A. McLean s.n.* (DAO); E end of Durrance Lake, Vancouver Island, 134 m, 18 Jul 1967, *A.S. Harrison 37.2* (CAN); McLeod Lake, 2250 ft, 19 Jul 1967, *V.J. Krajina & Revel s.n.* (UBC); Vancouver Island, Strathcona Provincial Park, 9 Sep 1967, *K. Beder, V. Bedanr, S. Kojima & V.J. Krajina s.n.* (UBC); Vancouver Island, Mill Hill, near Langford, 1 Jul 1969, *J.H. Soper, M.J. Shchepanek & A.F. Szczawinski 12243* (CAN); Vancouver Island, MacMillan Park, near Cameron Lake, 650 ft, 8 Jul 1969, *J.H. Soper, M.H. Shchepanek & A.F. Szczawinski 12403* (CAN); Strathcona Provincial Park, 250 m, 8 Jul 1969, *S. Kojima s.n.* (UBC); Upper Sage Creek Valley, 5200 ft, 20 Jul 1970, *K.I. Beamish, M. Bell & N. Anderson 756* (UBC); upper Sage Creek, 20 Jul 1970, *K. Beamish, M. Bell & N. Anderson 756* (CAN); Mount Revelstoke Robson Park, 3350 ft, 20 Aug 1970, *V.J. Krajina s.n.* (UBC); National Park, along Trail no. 10, mile 7, Summit Road, 3,750 ft, 30 Jul 1970, *J.H. Soper & M.J. Shchepanek 12740* (CAN); Mount Revelstoke National Park, W Woolsey Creek (Silver Creek), along trail no. 6, W Fork Woolsey Trail, 3 Aug 1970, *J.H. Soper & M.J. Shchepanek 12809* (CAN); Glacier National Park, Bald Mountain Trail to Grizzly Creek, at Beaver River crossing, 3600 ft, 27 Jul 1972, *E. Haber & M.J. Shchepanek 1634* (CAN); Manning Park, Poland Lake area, 1768 m, 7 Aug 1973, *C.C. Chuang 1056* (CAN); Point No Point, 23 Jul 1974, *Hainault & Tanguay 7691* (DAO); ca. 25 mi NW of Prince George on the N bank of the Fraser River, along the apex of its "big bend", 2000 ft, 30 Jul 1974, *V.J. Krajina, J. Pojar & C. Parsons s.n.* (UBC); Quesnel

Region, 17 mi E of Quesnel on Barkerville Road, 17 Jul 1976, *M. Barkworth 1634* (DAO); C.F.B. Kamloops, Mt Lolo, 22 Jul 1976, *M. Barkworth 1742* (DAO); Power River, W coast of Vancouver Island, 26 Jun 1979, *C.E. Jones s.n.* (DAO, UBC); W central Vancouver Island, 195 m, 20 Jun 1980, *D. Gagnon & G. A. Spiers 80-60-11* (UBC); Mt Lolo, 3 Jul 1980, *B. Brookes 1171* (DAO); Vancouver Island, Shawnagan Lake Port Renfrew Road ca. 12 mi W of Shawnagan Lake, 2 Aug 1980, *H.L. Dickson, M. Piche, D. Moennich, C. Barnard & R. Barnard 3790* (DAO); Lolo Mtn, 12 km E of Kamloops, 23 Aug 1980, *B.M. Brooke s.n.* (DAO); Vancouver Island, Goldstream Provincial Park, 30 Jun 1982, *S.G. Aiken, S.J. Darbyshire & L.E. Pavlick 2104* (DAO); W coast Vancouver Island, Pachena Bay, SW of Bamfield, West Coast Trail, 7 Jul 1982, *S.G. Aiken, S.J. Darbyshire & L.E. Pavlick 2214* (DAO, UBC); E of Kersley on Hwy 97, S of Quesnel, 2400 ft, 14 Jul 1982, *S.G. Aiken, S.J. Darbyshire & A. Roberts 2321* (DAO); Cariboo District, Timothy Mountain near Lac La Hache, 5454 ft, 18 Jul 1982, *S.G. Aiken & S.J. Darbyshire 2389* (DAO); E side of Matthew River, 930 m, 17 Aug 1982, *L.E. Pavlick 82-346* (V); Lower Fraser Valley, Mount McGuire, NE ridge, 6 Sep 1984, *Ceska 18066* (UBC); Goldstream Provincial Park, E side of Finlayson Arm, just outside park boundary, 30 Jun 1988, *S.J. Darbyshire 3739* (CAN); Saltspring Island, S end, Musgrave Road to Mount Bruce, 3 Jul 1988, *S.J. Darbyshire & J. A. Darbyshire 3769* (CAN, DAO); Skye Meadows Ecological Reserve, SE of Chilliwack, 2 Jul 1989, *G.B. Straley, R. Klinkenberg & B. Klinkenberg 5561* (UBC); Vancouver Island, Goldstream Park, 31 Aug 1993, *J. Cayouette & S.J. Darbyshire C7503* (DAO); Vancouver Island, 2-3 km E of Lizard Lake, 2 Sep 1993, *J. Cayouette, S.J. Darbyshire & L.E. Pavlick C7516* (DAO); Vancouver Island, Port Alberni, near mouth of Somass River, 11 Sep 1993, *J. Cayouette C7586, C7600* (DAO); Queen Charlotte Islands: Moresby Island, 6 km SSE of Sandspit, roadside next to Blaine Ck., 3 m, 18 Jul 1997, *F. Lomer & N. Grove 97403* (UBC); campground at Dragon Lake, 12 mi NE of New Aiyansh on road towards Cranberry Junction, 22 Jul 2004, *P.M. Peterson, J.M. Saarela & S. Smith 18694* (CAN, US); 9 mi NE of New Aiyansh on road towards Cranberry Junction, 22 Jul 2004, *P.M. Peterson, J.M. Saarela & S. Smith 18699* (CAN, US); Maroon Mountain Trail from end of road to ridge top, 23 Jul 2004, *P.M. Peterson, J.M. Saarela & S. Smith 18726* (US, UBC); Mayne Island, Bennett Bay, Gulf Islands National Park Reserve of Canada, Wilkes Road off Bennett Bay Road, 3 Jun 2007, *J.M. Saarela, D.M. Percy & Y. Chang 822* (CAN, UBC); Vancouver Island, Saanich Peninsula, at corner of Derrick Road and Norris Road, S of Deep Cove, 4 Jun 2007, *J.M. Saarela, D.M. Percy & Y. Chang 838* (CAN, UBC); Vancouver Island, Thetis Lake Regional Park, just N of Hwy 1, N of Langford, 4 Jun 2007, *J.M. Saarela, D.M. Percy & Y. Chang 853* (CAN, UBC); Vancouver Island, along Deering Road ca. 3 km N of Port Renfrew, 5 Jun 2007, *J.M. Saarela, D.M. Percy & Y. Chang 886* (CAN, UBC); Vancouver Island, 7.9 km along Horne Lake Road W of Hwy 19, 8 Jun 2007, *J.M. Saarela, D.M. Percy & Y. Chang 975* (CAN, UBC); Queen Charlotte Islands, Graham Island, Towhill Ecological Reserve, along small ecozone road to beach, Naikoon Provincial Park, 22 Jul 2007, *J.M. Saarela & D.M. Percy 1169* (CAN, UBC); Queen Charlotte Islands, Moresby Island, 21.5 km SW of Sandspit, E of Skidegate Lake, 0.3 km W of bridge at km marker 13, 2.2 km W of Y junction, 25 Jul 2007, *J.M. Saarela & D.M. Percy 1294* (CAN, UBC); Queen Charlotte Islands, Moresby Island, 12.7 km S of Sandspit, 25 Jul 2007, *J.M. Saarela & D.M. Percy 1296* (CAN, UBC); Queen Charlotte Islands, Moresby Island, 11.2 km S of Sandspit, adjacent to Copper Bay, 25 Jul 2007, *J.M. Saarela & D.M. Percy 1300* (CAN, UBC); W of Smithers, along Hudson Bay Mountain Road, between Smithers and alpine ski area, *J.M. Saarela & D.M. Percy 1344* (CAN, UBC).

Notes on Excluded Species

There is a single, early collection of *B. arvensis* L. (field brome) from British Columbia [Invermere, 29 Jul 1915, *M.O. Malte 108375* (CAN!, DAO!)]. In his distribution maps, Pavlick (1995) indicated that *B. arvensis* occurs in British Columbia, probably based on this collection. The annual *B. arvensis*, a species classified in *B.* sect. *Bromus*, is native to Europe; it occurs in scattered locations across North America, more commonly in the eastern U.S.A. (Pavlick & Anderton 2007). It is not known if *B. arvensis* species persists in British Columbia; it therefore is not formally treated here. Should the species be collected again in British Columbia, it can be distinguished from other *B.* sect. *Bromus* species in the province as follows: anthers 2.5–5 mm [vs. anthers < 2.5(–3) mm]; linear-lanceolate spikelets that narrow only slightly towards their apex [vs. ovate-lanceolate spikelets that narrow conspicuously towards their apex]; lower leaf sheaths with dense, softly appressed hairs 0.4–0.6 mm long [vs. lower leaf sheaths glabrous, sparsely to densely pilose with stiff hairs 0.5–0.6 mm long, or with soft and wavy hairs to 1.2 mm long]; and often purple-tinged spikelets (this colouration is not always present in dried specimens).

Taylor and Macbride (1977) reported *B. rubens* L. [=*B. madritensis* subsp. *rubens* (L.) Husn.] from British Columbia. Following this report, Salo (2005) indicated that red brome occurs in British Columbia, but she did not include any specimens on her distribution maps. There is a single collection of this species from British Columbia, collected over a century ago (Nanaimo, Vancouver Island, 13 Jul 1893, *Macoun 118* CAN-39043!, photo: DAO-56101!). The species seems not to have persisted in British Columbia and it is therefore not treated here.

Scoggan (1978:252) noted that *B. orcuttianus* Vasey had been previously reported from near Victoria, Vancouver Island. *Bromus orcuttianus* does not occur in British Columbia (see Saarela et al. 2005).

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MUNROCHLOA, A NEW GENUS (POACEAE: BAMBUSOIDEAE) WITH A NEW COMBINATION FROM INDIA

Muktesh Kumar and M. Remesh

Forest Ecology and Biodiversity Conservation Division
Kerala Forest Research Institute
Peechi, 680 653, Thrissur, Kerala, INDIA
muktesh@kfri.org

ABSTRACT

Munrochloa (Poaceae: Bambusoideae) a new genus is erected and described here based on a bamboo, which formerly was described under the genus *Oxytenanthera* Munro. A new combination, **Munrochloa ritchiei** (Munro) M. Kumar & Remesh, comb. nov., is proposed.

RESUMEN

Munrochloa (Poaceae: Bambusoideae) se erige como un nuevo género y se describe aquí basado en un bambú, que se describió previamente en el género *Oxytenanthera* Munro. Se propone una nueva combinación, ***Munrochloa ritchiei*** (Munro) M. Kumar & Remesh, comb. nov.

INTRODUCTION

While working on revisionary studies of the genera *Oxytenanthera* Munro, *Pseudoxytenanthera* Soderstr. & Ellis, it was observed that *Pseudoxytenanthera ritchiei* (Munro) Naithani, possessed characters not included in the genus *Pseudoxytenanthera*. Detailed morphological studies revealed that the species possesses a number of unique characters which are very distinct from the generic characters of *Oxytenanthera* and *Pseudoxytenanthera*. Therefore, we are erecting a new genus to accommodate the species.

It was Colonel Munro (1868) who first described the new species in his monograph on *Bambusa*. *Bambusa ritcheyi*, was based on a herbarium specimen collected by J.C. Ritchie from Kala Nuddi, Bombay, India. In the addenda of the same publication, Munro corrected the spelling of the ritcheyi to 'ritchiei' to commemorate Ritchie's name. After a lapse of five years Beddome (1873) collected this bamboo from Anamalai and included it under the genus *Oxytenanthera* Munro. Due to the presence of a monostigmatic ovary, Beddome named this species as *Oxytenanthera monostigma*. This species was subsequently reported by various workers from Western Ghats, hills of south west India from Mahabaleshwar to Anamalai up to Palakkad gap such as Brandis from Sattara Ghats in 1870; R.S. Fagan at Mahabaleshwar in 1892; WA. Talbot from North Canara in 1884 and 1889; R.C. Wroghton, from Pune district and A.D. Wilkins from Ahamed Nagar in 1892 (Gamble 1896). Gamble stated that Munro himself had also agreed with the new treatment as *Oxytenanthera monostigma*. Later, Brandis (1906) and Bourdillon (1908) followed this treatment. Gamble, noted that the species has very well-marked velvety culms, a narrow culm sheath, long narrow spikelets with only one flower, and a glabrous ovary and style. While working on this species at a later day, Gamble commented, "I am rather in doubt whether Munro's specific name should not have precedence". And this doubt was clearly noted by Blatter and McCann (1929) and provided a new combination *Oxytenanthera ritchiei* (Munro) Blatt. & McCann. Without considering the corrected species name as *'ritchiei'*, several workers erroneously spelled the epithet as *ritcheyi* in their publications. Nayar and Ansari (1982) also followed the species name spelling it *ritcheyi*.

While preparing an account of the enumeration of Indian monocotyledons, Majumdar (1989) came to the conclusion that the Indian species of *Oxytenanthera* do not fit the generic description of *Oxytenanthera*. He erected a new genus, *Pseudotenanthera*, to include species having sub-scandent to scandent branches in tufts, no resting central bud, a thin solid style, a pericarp thin and separable from seed, and made a new combination *Pseudotenanthera ritcheyi* (Munro) R. Majumdar.

Subsequently, Naithani (1990) treated *ritcheyi* in the genus *Pseudoxytenanthera* of Soderstrom and Ellis

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(1988) to accommodate *Oxytenanthera monadelpha* (Thwaites) Alston which has a vine like culm, numerous basal branches, capitate cluster of spikelets, and six stamens. Naithani (1990) maintained that Majumdar's new genus, *Pseudotenanthera,* coincidentally possesses similar characters of *Pseudoxytenanthera* Soderstr. & Ellis. Therefore, Naithani considered the genus a superfluous name and transferred all the species known of *Oxytenanthera* from India to the genus *Pseudoxytenanthera* Soderstr. & Ellis.

During revisionary studies on Indian Bamboos the authors conducted a detailed comparative account on generic characters of *Oxytenanthera*, *Pseudoxytenanthera* and noted that the *Pseudoxytenanthera ritchiei* (Munro) Naithani, possesses a number of distinct characters such as, completely solid culms, prophyllum buds without keels, inflorescence with strongly capitate heads, with leaf sheaths, palea without keels, and a monostigmatic ovary. The other species treated under the genus *Oxytenanthera* possesses hollow culms, keeled prophyllum of buds, semicapitate heads without leaf sheaths, palea two keeled, and three stigmas. The distinguishing characters of the species also were compared with other genera of the sub tribe Bambusinae such as *Dendrocalamus*, *Bambusa* and *Gigantochloa* It has been noted that the diagnostic characters like solid culms clothed with silky white tomentum; prophyllum buds and palea without keel; monostigmatic ovary, and united filaments, together make this species distinct and therefore, belongs under a new genus *Munrochloa*.

Inter generic affinities

The genus *Munrochloa* shows some affinities with *Dendrocalamus*, *Oxytenanthera*, *Pseudoxytenanthera* and *Gigantochloa*. (Table 1). The habit and habitats of this taxon resembles *Denrocalamus stocksii* and *Dendrocalamus strictus* both having thick walled culms for those clumps especially growing in dry areas. Though *Munrochloa ritchiei* grows even in fully irrigated areas have fully solid culms. The nature of inflorescence is almost similar to *Dendrocalamus*, *Oxytenanthera* and *Pseudoxytenanthera* but in *Munrochloa* spikelets clusters are usually supported with leaf sheaths. The spikelets are single flowered. The palea of all the other members in the subtribe Bambusinae is two-keeled. In *Munrochloa* palea is without any keels. The stigma of the species of *Oxytenanthera* and *Pseudoxytenanthera* is divided in to three and *Munrochloa* has a monostigmatic ovary similar to Dendrocalamus and *Gigantochloa*. The inter generic affinity of the *Munrochloa* shows that there is an interlink between *Dendrocalamus* and *Oxytenanthera* and also having distinct generic status with few key characters like, imperfectly keeled prophyllum buds, fully solid culms, palea without any keels.

KEY TO *MUNROCHLOA* AND ALLIED GENERA

1. Bamboo floret with undivided stigma.
   2. Culms fully solid, midculm prophylls and palea not keeled ____ **Munrochloa**
   2. Culms hollow, midculm prophylls and palea keeled.
      3. Inflorescence strongly packed in semiverticellate clusters of spikelets, filaments of the anther free ____ **Dendrocalamus**
      3. Inflorescence loosely packed in semiverticellate clusters of spikelets, filaments of the anther united ____ **Gigantochloa**
1. Bamboo floret with stigma divided into three.
   4. Bamboos erect ____ **Oxytenanthera**
   4. Bamboos scandent or climbing ____ **Pseudoxytenanthera**

Munrochloa M. Kumar & Remesh, gen. nov. Typus species: *Munrochloa ritchiei* (Munro) M. Kumar & Remesh.

Oxytenantherae similes in aspectu et inflorescentiae modo, culmis fere solidis tomento albo-sericeo tectis, prophylli gemmis in culmo mediali imperfecte carinatis, palea ecarinata, ovario monostigmateo differt.

An erect medium sized gregarious, bamboo forming loose clumps. Rhizome is sympodial. Culms are erect and solid. Prophyllum imperfectly keeled. Culm sheaths narrow, conical in shape. Branches are almost equal size. Leaves arise on branches. Inflorescence a large compound spicate, terminal panicle, arises on the nodes of branches as dense globose heads associated with leaf sheaths. Spikelets usually single flowered, sometimes 2, lanceolate, Lemma linear-lanceolate, glabrous. Palea membranous, glabrous, not keeled. Stamens 6,

Table 1. A comparison of Munrochloa with allied genera.

Characters	*Dendrocalamus*	*Gigantochloa*	*Oxytenanthera*	*Pseudoxytenanthera*	*Munrochloa*
Habit	Erect	Erect	Erect	Scandent and semiclimbing	Erect
Rhizomes	Sympodial short necked	Sympodial short necked	Sympodial long or short necked	Sympodial short necked or long necked	Sympodial long necked
Culm	Hollow/Solid	Hollow	Hollow	Hollow	Strictly solid
Culm surface	Smooth and glabrous	Smooth and glabrous	Smooth and glabrous	Smooth and glabrous	Rough and tomentose
Culm sheath auricle	Well developed with or without oral setae	Well developed with or without oral setae	Well developed without oral setae	Well developed with oral setae	Absent or rudimentary without oral setae
Mid culm prophylls	2 keeled	2 keeled	2 keeled	2 keeled	Not keeled
Inflorescence branching and presence of leaf sheath	Strongly capitate and leaf sheath absent	Loosely capitate, few in a head and leaf sheath absent	Strongly capitate and leaf sheath rarely present	Strongly capitate and leaf sheath absent	Strongly capitate and leaf sheaths are prominent
Spikelets	2–3-flowered	2–4-flowered	1–3-flowered	2-flowered	Single flowered
Lemma	Sparsely hairy	Glabrous or sparsely hairy	Sparsely hairy	Sparsely hairy	Glabrous
Palea	2 keeled	2 keeled	2 keeled	2 keeled	Not keeled
Lodicules	Absent	Mostly absent but present in few species	Absent	Absent	Absent
Anther filaments	Free	United	United	United	United
Style	Long and hairy	Long and hairy	Long and hairy	Long and hairy	Long and hairy
Stigma	Single	Single	Three	Three	Single
Fruit	Globose caryopsis	Cylindric or ellipsoid caryopsis	Ellipsoid caryopsis	Ellipsoid caryopsis	Ellipsoid caryopsis

monadelphous, strongly apiculate. Ovary glabrous, ovate; stigma single, curved plumose. Fruit a caryopsis, linear-oblong, faintly grooved with a small beak.

Similar to *Oxytenanthera* Munro in general appearance and inflorescence type but differs in presence of solid culms clothed with silky white tomentum on the surface, imperfectly keeled mid culm prophyll buds, palea without keels and monostigmatic ovary.

Etymology.—The generic name is to commemorate the name of Colonel William Munro (1818–1880), who had contributed the most valuable monograph on Bamboos of the world. This genus is represented only with a single species and endemic to Western Ghats of India.

Munrochloa ritchiei (Munro) M. Kumar & Remesh, comb. nov. (**Fig. 1**). *Bambusa ritchiei* Munro, Trans. Linn. Soc. London 26:157. 1868. *Oxytenanthera ritchiei* (Munro) Blatt. & McCann, J. Bombay Nat. Hist. Soc. 33:773. 1929, "ritcheyi"; V.J. Nair & R. Ansari, J. Econ. Tax. Bot. 3:616. 1982. *Pseudotenanthera ritchiei* (Munro) R.B. Majumdar in Karthikeyan et al., Fl. Ind. ser. 4, 2(Enum. Monocotyl.): 280. 1989. *Pseudoxytenanthera ritcheyi* (Munro) H.B. Naithani, J. Bombay Nat. Hist. Soc. 87:440. 1990; D.N. Tewari, Monogr. Bamboo 127. 1992; K.K. Seethal. & M. Kumar, Bamboos India 225. 1998. *Pseudoxytenanthera ritchiei* (Munro) Ohrnb., Bamboos World 313. 1999, an isonym. Type: INDIA: Bombay, Kala Nuddi, *J.C. Ritchie* 820 (lectotype, here designated: K).

Oxytenanthera monostigma Bedd., Fl. Sylv. S. India 3:233. 1873. Gamble, Ann. Roy. Bot. Gard. Calcutta 7:74, t. 65. 1896 & in Hook. f., Fl. Brit. India 7:402. 1897. Brandis, Indian Trees 674. 1906. Bourd., Forest Trees Travancore 400. 1908. C.E.C. Fisch. in Gamble, Fl. Madras 3:1861. 1934. Type: INDIA: Anamalai, *R.H. Beddome s.n.* (holotype: K)].

Vernacular names.—Choomaree, chiwa, chiwan, Huda, manga, udhe, thandali (Marathi) Erankol and Korna (Malayalam)

Specimens examined: **INDIA. KARNATAKA:** Uttara Kannda Dist. *s. loc.*, 1884, *WA Talbot 583* (BSI); Feb 1889 *WA Talbot 906* (CAL); Dandeli, 21 Jan 1924, *RN Sarkar 2142* (DD). **KERALA:** Kannur Dist. Panathur, 28 Jan 1979, *VJ Nair 59948* (MH); 28 Jan 1979, Panathady, 28 Jan 1979, *VS* Ramachandran *59291* (MH). Malappuram Dist. Nilambur, 11 Feb1934, *HG Champion 1135* (DD); Manikkamudy, 6 Feb 2001, *M Remesh & N Unnikrishnan 20650* (KFRI); Vazhikkadavau, 7 Aug 1983, *Philip Mathew 34163* (CALI). Palakkad Dist. Manthanpotti, 20 Nov 1999, *M. Kumar & Stephen Sequiera 20635* (KFRI).

Distribution and ecology.—This species is endemic to Western Ghats. It is distributed in northern Kerala and Karnataka. It was also reported from Maharashtra. It is found growing from an altitude of 200–1100 m. It is a component of moist deciduous forests and also found as pure patches. Sporadic flowering is common during summer months. Gregarious flowering was observed in the year 2001 at Nilambur forests, Malappuram district, Kerala.

Conservation status.—This potential bamboo of south India is extracted for various uses. The recent study by the authors revealed that the species is Conservation Dependent as per the IUCN standards and needs appropriate conservation and management strategies for a sustainable utilization of this species.

Uses.—The solid culms of this bamboo are used for making furniture, lathi, etc. It is also used as a support for betal plants, for making baskets, umbrella handles and walking sticks.

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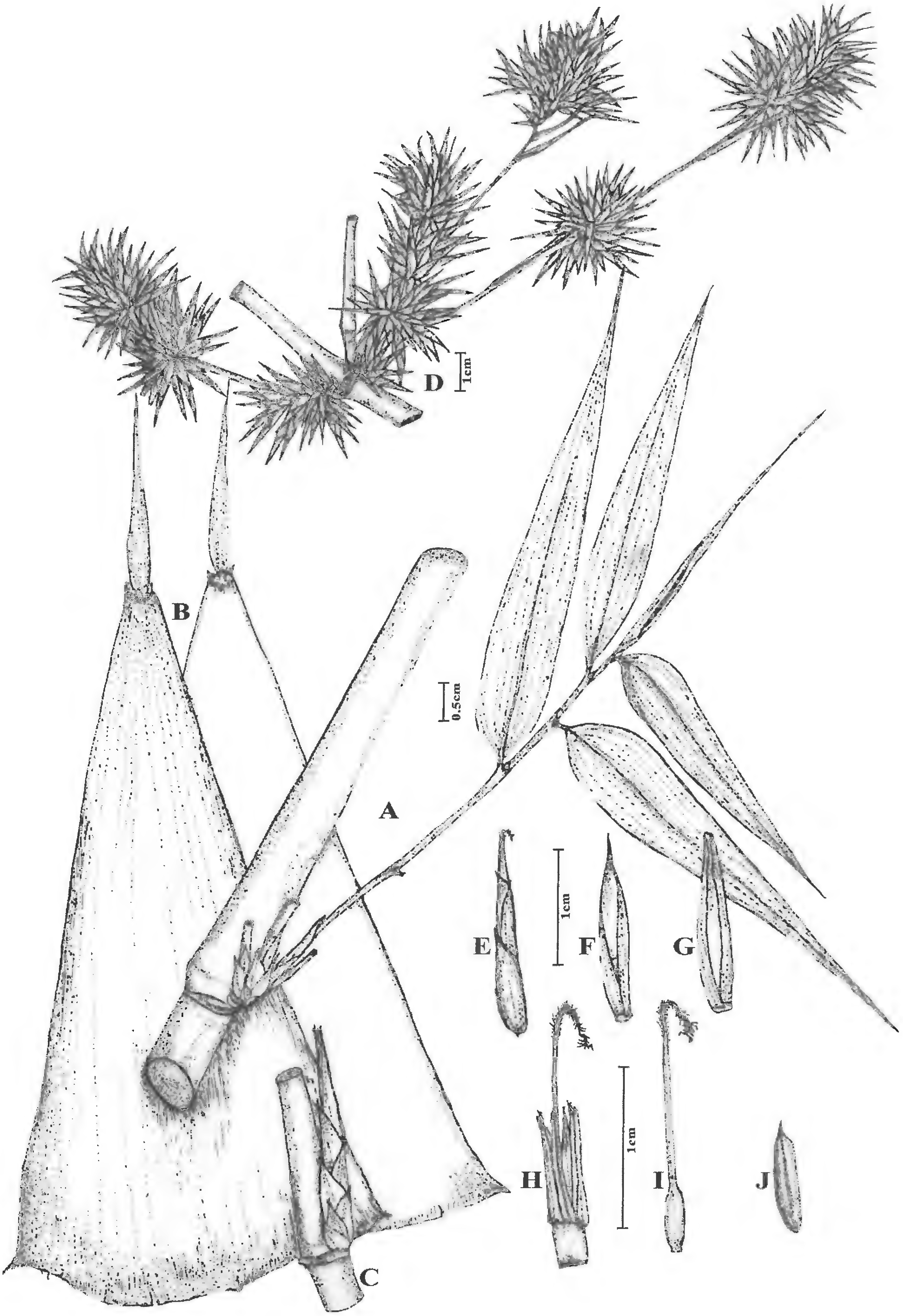

Fig. 1. *Munrochloa ritchiei*. **A.** Solid culm with leafy branches; **B.** Culm sheath dorsal and ventral view; **C.** Nodes with buds; **D.** Inflorescence; **E.** Spikelet; **F.** Lemma; **G.** Palea; **H.** Floret; **I.** Style; **J.** Fruit.

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TWO NEW SPECIES OF CYPERACEAE FROM PENINSULAR INDIA

M.A. Wadood Khan
Department of Botany
Majalgaon Arts, Science & Commerce College
Majalgaon–431131, District: Beed
Maharashtra, INDIA

P. Lakshminarasimhan
Central National Herbarium
Botanical Survey of India
P.O. Botanic Garden, Howrah-711103
West Bengal, INDIA

ABSTRACT

Two new species, **Cyperus karthikeyanii** (from Karnataka) and **Fimbristylis naikii** (from Maharashtra and Andhra Pradesh), are described and illustrated. Keys to distinguish the new species of *Cyperus* and *Fimbristylis* from their allied species are also provided.

RESUMEN

Se describen e ilustran dos especies de la familia Ciperáceas nuevas para la ciencia: ***Cyperus karthikeyanii*** (procedente de Karnataka), y ***Fimbristylis naikii*** (de Maharashtra y Andhra Pradesh). Adicionalmente se proporciona una clave para separar los nuevos taxa de sus parientes cercanos en los géneros *Cyperus* y *Fimbristylis*.

INTRODUCTION

The genera *Cyperus* L. and *Fimbristylis* Vahl consist of ca. 300 and 250 species respectively and are distributed in tropical and warm regions of the world (Mabberley 1997). Karthikeyan et al. (1989) in his enumeration of Monocotyledons, listed 86 taxa (71 species) of *Cyperus* and 102 taxa (90 species) of *Fimbristylis* from India.

During the course of botanical explorations of the tropical evergreen forests in the Western Ghats, two interesting specimens belonging to Cyperaceae were collected viz., *Cyperus* (Section *Mariscus*) and *Fimbristylis* (Section *Fimbristylis*, Series Dichotomae). Based on a perusal of the literature, comparison with the herbarium collections at Herbarium of Cyperaceae, Majalgaon College, Majalgaon (HCMCM), BSI & CAL, and our own field observations, the specimens were found to be very distinct and both are described here as new species viz., *Cyperus karthikeyanii* and *Fimbristylis naikii*.

1. Cyperus karthikeyanii Wad. Khan & Lakshmin., sp. nov. (**Fig. 1**). Type: INDIA. Karnataka State: Udupi, 20 Sep 1999, *Sardesai s.n.* (HOLOTYPE: CAL; ISOTYPES: HCMCM, K).

Cyperus clarkei T. Cooke et *C. panicei* (Rottb.) Boeck. habitu stolonifero caulibus ad basin cormo similibus, spiculis unifructis, gluma fructifera involuta dorsaliter rotundata affinis, sed habitu tenuissimo, stolonibus tuberiferis tenuibus atque reliquiis fibrosis obtectis, spicis brevioribus (4–6 mm), nucibus aliquantum longioribus (ca. 2.5 mm) et staminibus 3 ab ambabus speciebus valde differt.

Perennials, 15–35 cm tall with tuberiferous stolons; stolons slender, wiry, 1–2 cm long, 1.25–1.5 mm thick, covered with purple-brown, strongly nerved, ovate or ovate-lanceolate scales (2.5–4 × 1–2.5 mm) which soon become fibrous; tubers ellipsoid, purple-brownish, 4–5 mm long and broad, covered with fibrous remains; stem trigonous, filiform to rather slender, 0.5–0.7 mm thick, glabrous, with often corm like or enlarged base. Leaves basal, 0.5–1 mm wide, flexuous, shorter to, as long as or rarely overtopping the stems, scaberulous on margins in upper half, caudate-tipped; sheath pale to dark purple-brownish, fibrous with age. Inflorescence of single, terminal capitate head of 2–5 sessile clustered spikes under 1 cm long and broad; involucral bracts 3–5, 1–2 setiform, the others foliaceous, the longest one 6–20 cm long, spreading or sub-erect, glabrous, subcylindricaly oblong, 4–5 mm long, greenish with up to 15 spikelets. Spikelets trigonous, ellipsoid, deciduous, 3.8–4 × 0.5–0.7 mm, narrowed towards both the ends, curved, whitish, tinged with purple near base or purple dotted, one flowered. Glumes 4, empty glumes 2, persistent on rachilla, broadly hyaline margined, unequal, the larger one broadly to suborbicular-ovate, ca. 1 mm long, several nerved, the second smaller one lanceolate; fruiting glumes 2, subequal, the basal one 3.8–4 × 0.7 mm, enrolled, tightly wrapping the nut, multinerved, herbaceous, acute, rounded on the back, the upper one narrowly

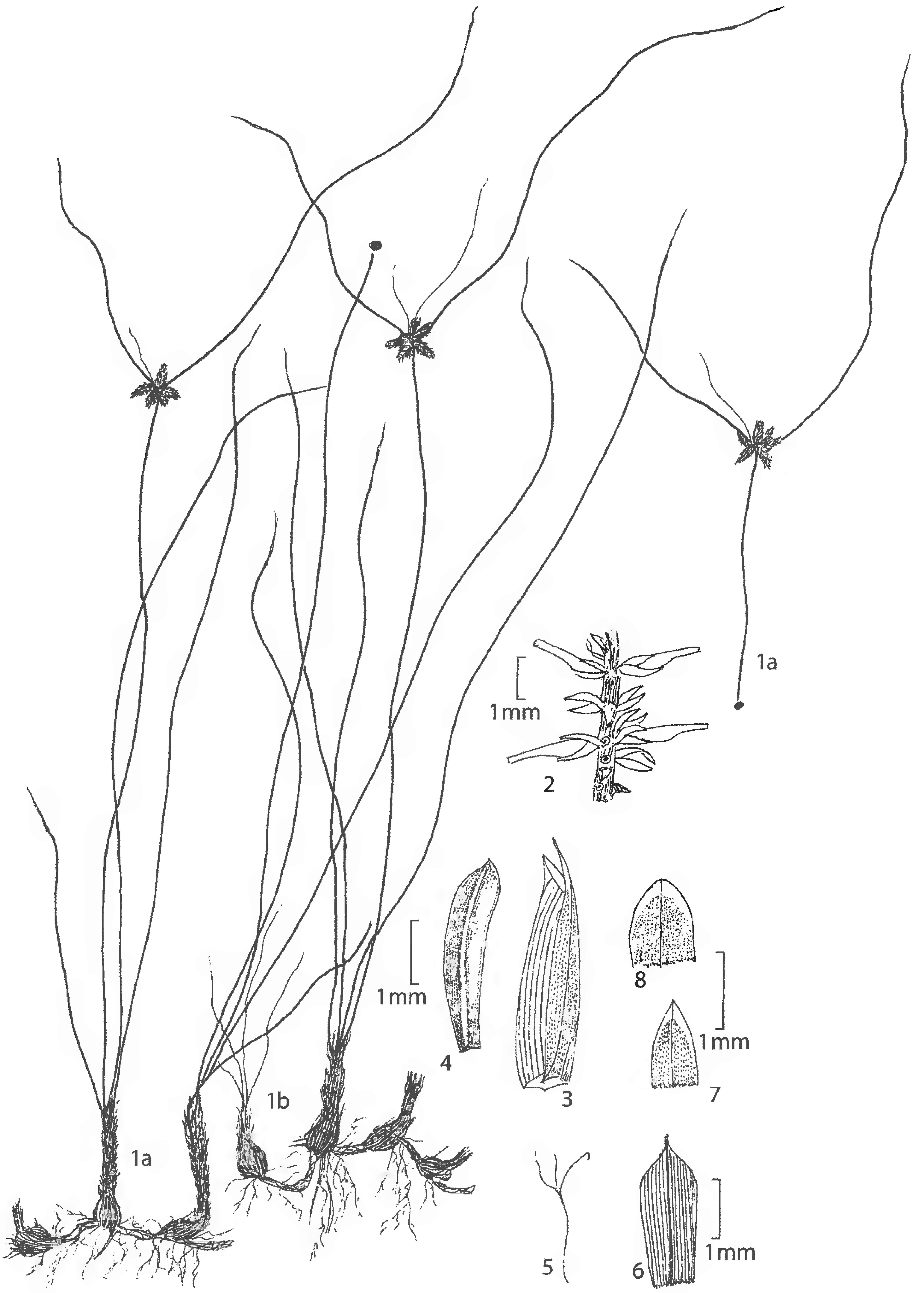

Fig. 1. *Cyperus karthikeyanii* Wad. Khan & Lakshmin. 1a–b. Habit; 2. Spike with spikelets and persistent empty glumes; 3. Spikelets with fruiting glumes; 4. Nut; 5. Style with stigmas; 6. Stolon scale; 7–8. Empty glumes.

lanceolate, hyaline, uninerved, acuminate (with awn-like tip). Stamens 3. Styles 3–fid, filiform, 0.8–1 mm long, glabrous; stigmas shorter than the styles. Nuts acutely trigonous, ellipsoid-oblong, 2.4–2.5 × 0.4–0.6 mm, curved, narrowed towards both the ends, pale orange-yellow, puncticulate with isodiametric epidermal cells; gynophore obscure.

In its stoloniferous habit with usually corm-like base of stems, the one fruited spikelets and involute fruiting glume with rounded back, it shows affinities with *Cyperus clarkei* T. Cooke and *C. paniceus* (Rottb.) Boeck. but differs essentially by the extreme slender habit, the tuberiferous slender stolons covered with fibrous remains, the smaller (4–6 mm long) spikes, the some what longer nuts (ca. 2.5 mm) and the 3 stamens.

Habitat and ecology.—Occasional under shade of thick semi-evergreen forests (1000 m above m.s.l.).

Flowering and fruiting.—September-November.

Etymology.—This species has been named after Dr. S. Karthikeyan (ex Deputy Director, Botanical Survey of India) in appreciation of his contribution to the field of systematic botany.

PARATYPES: **INDIA. KARNATAKA STATE:** Londha Forest, 27 Nov 2000, *Khan 4759* (HCMCM); Ramnagar Forest, 22 Nov 2007, *Khan 1205* (HCMCM).

KEY TO NEW AND ALLIED SPECIES

1. Stolons tuberiferous, 1–2 cm long; stems and leaves filiform to rather slender, 0.5–0.7 mm thick; spikes 4–5(–6) mm long; nuts ca. 2.5 mm long **C. karthikeyanii**
1. Stolons etuberiferous, 5–10 cm long; stems and leaves not filiform or if stems sometimes slender (0.5–1 mm thick in *C. paniceus* var. *paniceus*) the leaves (1–)2–6 mm wide; spikes 8–15 mm long; nuts 1.5–2.2 mm long.
   2. Stems distinctly quasi bulbosely thickened at base; leaf-sheaths straw colored; rays of inflorescence if present up to 4 mm long; nuts 1.5–1.7 mm long **C. clarkei**
   2. Stems not or slightly bulbose at base; leaf-sheaths often purplish; rays if present up to 4 cm long; nuts 1.8–2.2 mm long **C. paniceus**

2. *Fimbristylis naikii* Wad. Khan & Lakshmin., sp. nov. (**Fig. 2**). TYPE: INDIA. MAHARASHTRA: Kolhapur-Amboli Road, 18 Oct 1995, *Khan 4341* (HOLOTYPE: CAL; ISOTYPES: BSI, HCMCM, K).

Fimbristylis tomentosae Vahl valde similis sed gynophoro minore plerumque rufo-brunneo, 0.1–0.2(–0.3) mm longo latoque, nuce late obovoidea atque in superficie ordinatim subtrabeculata tuberculata, ordinatione e seriebus 15–18 verticalibus cellularum epidermalium constante, nuce ad apicem subtruncata, mutica vel obscure apiculata, spiculis 3–9 in inflorescentiam minorem dispositis differt. Ad *F. dichotomam* (L.) Vahl etiam ut videtur accedit sed glumarum lateribus multinervibus, nucibus majoribus (1.2–1.6 × 0.8–1.2 mm) atque series plus quam 15 verticales cellularum parietibus tenuibus instructis epidermalium ferentibus differt.

Annuals, 10–35 cm tall; stems slender, trigonous to compressed trigonous, 0.3–1 mm thick, ribbed, glabrous, rather rigid. Leaves ligulate, subbasal, 1–2 mm wide, 1/2 to 3/4 or more as long as the stems, flat with often thick rib-like margins, hairy with long white cilia or glabrescent, acute; sheaths densely hairy, glabrous or glabrescent, pale ferrugineus or dark brownish. Inflorescence small, simple to subcompound, 1.5–3.5 cm long and broad with usually 3–9 spikelets; rays if present 1–3, each one bearing usually paired (rarely 3) spikelets; involucral bracts up to 6, 1–2 foliaceous, the other ones setiform, the longest one as long as to much overtopping the inflorescence up to 6 cm long, long ciliate at least on margins and base. Spikelets all solitary, ovoid or ovoid-oblong, 3–7 × 2–3.5 mm, acute, brown-white variegated, many flowered; peduncles 2–5 mm long; rachilla winged. Glumes spiral, some what loosely imbricated, ovate to broadly ovate, 2–2.8 × 1.8–2.2 mm, almost as long as to slightly longer than broad, multistriate on sides, obtuse or acute, distinctly apiculate, often enrolled in fruiting, reddish-brown with whitish keel portion on the back, broadly hyaline margined; keel 3–5-nerved with strong mid nerve. Stamens 1 or 2; anthers elliptic-oblong, 0.4–0.5 mm long, apiculate. Styles flat, shorter than the nuts, 1–1.2 mm long, conspicuously broader than the staminal filaments, fimbriate throughout, not hyaline margined, pyramidally dilated at base or somewhat gradually narrowed upwards; stigmas shorter than the styles, shortly hairy. Nuts biconvex, broadly obovoid, 1.5–1.6 × 0.8–1.2 mm, turgid in the centre, subtrabeculate with 15–18 vertical striations in between transversely oblong thin walled epidermal cells, distinct in the centre and on the shoulder, nearly quadrate near base

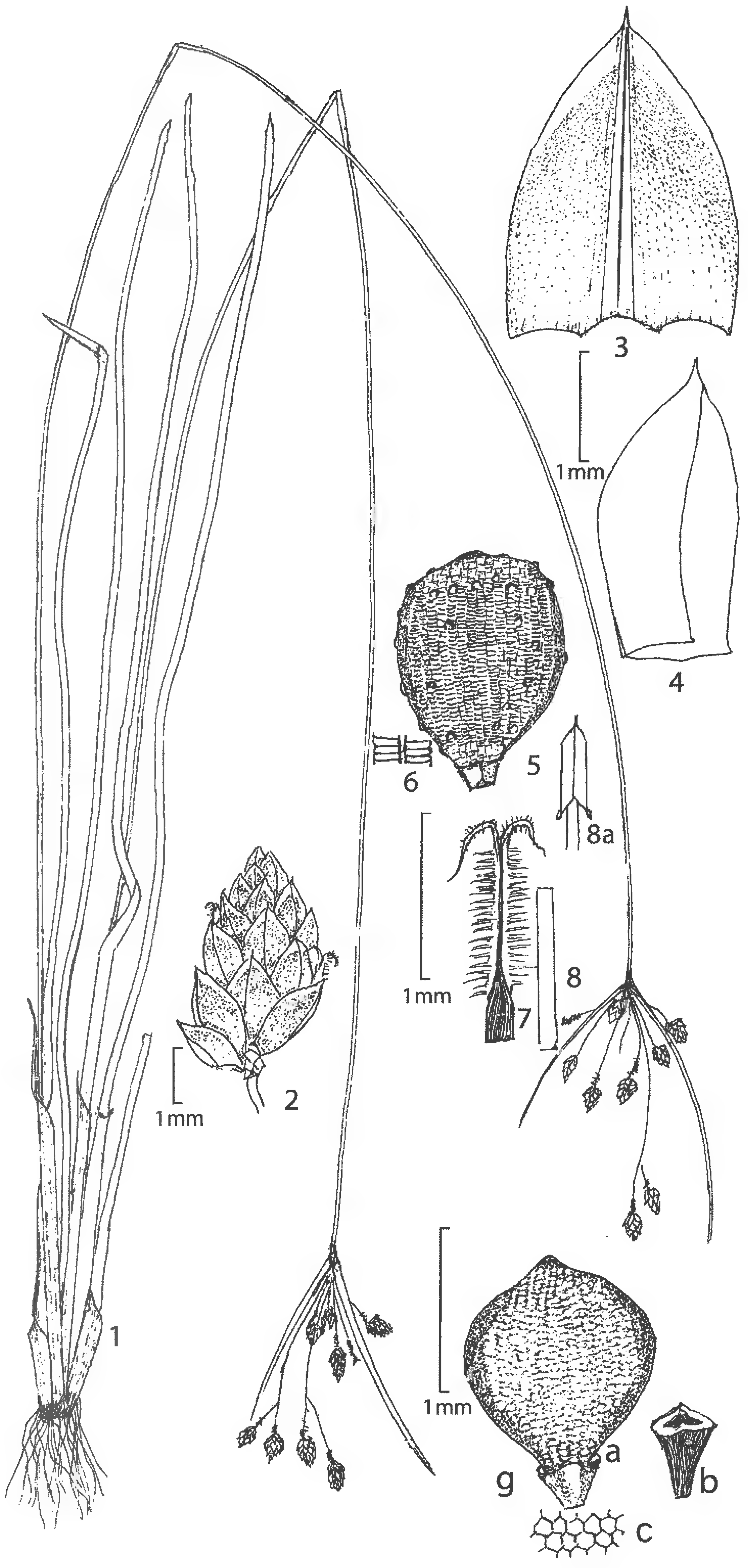

Fig. 2. *Fimbristylis naikii* Wad. Khan & Lakshmin. 1. Habit; 2. Spikelets; 3–4. Glumes; 5–6. Nut and epidermal cells; 7. Style; 8. Staminal filament; 8a. Stamen; 9a–c. *Fimbristylis tomentosa* Vahl – nut, gynophore and epidermal cells (for comparison).

and apex, and on shoulder, apex rounded to subtruncate, muticous; gynophore discoid or cupoid, small, 0.1–0.2(–0.3) mm long and broad, not or obscurely lobed, often reddish-brown (very rarely dull whitish), its thin rim often appressed to the nut base.

It is very similar to *F. tomentosa* Vahl but differs from the latter by the smaller, usually reddish-brown, 0.1–0.2(–0.3) mm long and broad gynophore, the broadly obovoid nut with subtrabeculate, tuberculate surface pattern with 15–18 vertical rows of epidermal cells, and subtruncate, muticous or obscurely apiculate apex together with 3–9 spikelets in smaller inflorescence. Apparently it also approaches *F. dichotoma* (L.) Vahl and differ in having many nerved sides of glumes, the larger (1.5–1.6 × 0.8–1.2 mm) nuts with more than 15 vertical rows of thin walled epidermal cells.

Habitat and ecology.—Occasional in wet open grassland and eutrophicated marshes.

Flowering and fruiting.—October-November.

Etymology.—The species has been named after Dr. V.N. Naik (teacher of senior author) in appreciation of his outstanding contribution in the field of taxonomy.

PARATYPES: **INDIA. MAHARASHTRA. Kolhapur District:** Shivaji University Campus, 18 Oct 1995, *Khan 4337a* (HCMCM); way to Gadhinglaj to Ajra, 11 Oct 2004, *Chavan 5314*, 5317 (HCMCM). **ANDHRA PRADESH. Medak District:** Patancheru, 30 Oct 2005, *Solanke 824* (HCMCM).

Notes.—This and other 3 taxa viz., *F. tomentosa* Vahl (= *F. podocarpa* sensu C.B. Clarke, 1893; = *F. dichotoma* (L.) Vahl subsp. *podocarpa* sensu T. Koyama, 1985; = *F. dichotoma* var. *pluristriata* sensu Napper 1971), *F. alboviridis* C.B. Clarke, and the African *F. striolata* Napper are very closely related to each other. Authors such as Clarke (1893), Kern (1974), Kral (1971), and a few others treated *F. tomentosa* distinct specifically from *F. dichotoma*.

With its smoothly subtrabeculate nut surface pattern having more than 15 fine close vertical striations or rows of thin walled cells and conspicuous tuberculations, *F. naikii* is very unlike to *F. dichotoma* or *F. merrillii* J. Kern, but somewhat approaches to *F. alboviridis* C.B. Clarke. The latter is distinguished by the smaller nuts (0.8–1 × 0.5–0.7 mm) and white-brown variegated nerveless glumes (ca. 2 mm long). The new species is undoubtedly more close to *F. tomentosa* and can be thus distinguished from the latter and other allies as under.

KEY TO NEW AND ALLIED SPECIES

1. Nuts with 15–24 fine close vertical striations or rows of thin walled epidermal cells, smoothly reticulate or subtrabeculate, usually large, 1.5–2.2 mm long; glumes distinctly nerved on sides.
   2. Gynophore large, 0.5–0.7 mm long, cupoid or obconical, often produced below, 3-lobed, whitish with thick rim distinguishable or not appressed to nut base; nuts broadly ellipsoid or suborbicular, 1.9–2.2 mm long, acutish at apex, etuberculate (rarely with 1–3 faint tubercles), reticulate from isodiametric hexagonal or rounded cells, arranged in 20–24 vertical rows or striations ____ **F. tomentosa**
   2. Gynophore small, 0.2–0.3 mm long, cupoid, not lobed, always brownish, with thin rim appressed to nut base (appearing continuation of nut-body); nuts broadly obovoid, 1.5–1.6 mm long, rounded to subtruncate at apex, densely tuberculate, subtrabeculate from some what transversely oblong or elliptic cells arranged in 15–18 vertical rows or striations ____ **F. naikii**
1. Nuts with 5–10(–12) vertical ridges or rows of thick walled transversely oblong (bar-like) epidermal cells, i.e. coarsely trabeculate, 0.8–1.2 mm long; glumes nerveless on sides.
   3. Style more or less hairy throughout the length, often hyaline margined; nuts usually etuberculate ____ **F. dichotoma**
   3. Styles glabrous or almost glabrous with sometimes few cilia at top, not hyaline margined; nuts mostly tuberculate ____ **F. merrillii**

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LYONOTHAMNEAE, A NEW TRIBE IN THE ROSACEAE (ROSALES)

Luc Brouillet

Herbier Marie-Victorin
Institut de recherche en biologie végétale
Université de Montréal
4101 rue Sherbrooke E
Québec, CANADA, H1X 2B2
luc.brouillet@umontreal.ca

ABSTRACT

Recent molecular phylogenetic analyses of Rosidae and Rosaceae, notably the Potter et al. (2007) paper, have led to changes in the circumscription and classification of Rosaceae. In the Potter et al. paper, *Lyonothamnus* was left outside any recognized tribe. It had been traditionally classified in Quillajeae; *Quillaja* is now a member of Quillajaceae (Fabales). A monogeneric tribe, **Lyonothamneae**, is erected to house *Lyonothamnus*.

ABSTRACT

Recientes análisis filogenéticos moleculares de Rosidae y Rosaceae, principalmente el artículo de Potter et al. (2007) han producido cambios en la circunscripción y clasificación de Rosaceae. En el artículo de Potter et al., *Lyonothamnus* se dejó fuera de cualquier tribu reconocida. Había sido clasificado tradicionalmente en Quillajeae; *Quillaja* es ahora uno de los miembros de Quillajaceae (Fabales). Se hace una tribu monogenérica, **Lyonothamneae**, para albergar a *Lyonothamnus*.

Molecular phylogenetic analyses of the angiosperms and, more specifically, of Rosidae Tahkht. (summarized in Angiosperm Phylogeny Group 2003) and Rosaceae Juss. (e.g., Morgan et al. 1994) have substantially changed our perception of the relationships of Rosaceae, and have resulted in slight changes to its circumscription. Traditional Rosales Bercht. & J. Presl (e.g., Cronquist 1981) included families that are now dispersed in many orders and subclasses (Angiosperm Phylogeny Group 2003). Rosales now has a circumscription that includes members of the former Rhamnales Linnk and Urticales Juss. ex Bercht. & J. Presl (Angiosperm Phylogeny Group 2003). Similarly, phylogenetic analyses have led to a new classification of the Rosaceae (Potter et al. 2007), with a reorganization of subfamilies and, to a lesser extent, tribes. Hypotheses of relationships among tribes and subfamilies were also considerably modified as a result of this analysis. One may compare, for instance, the traditional classification used by Kalkman (2004) to that of Potter et al. (2007): the classic subfamilies Spiraeoideae Arn., Rosoideae Arn., Prunoideae Horan., and Maloideae Weber, recognized in the former, were reduced to three in the latter, Rosoideae, Dryadoideae Sweet, and Spiraeoideae. The last subfamily now incorporates genera formerly included in three subfamilies, including Prunoideae and Maloideae. In the phylogenetic analysis of Potter et al. (2007), *Lyonothamnus* A. Gray appeared at the base of Spiraeoideae, sister to all other members of the clade. In their classification, *Lyonothamnus* was not assigned to a tribe. Historically, *Lyonothamnus* has been considered part of tribe Quillajeae Endl., along with *Quillaja* Molina. *Quillaja* is now treated as the only genus in Quillajaceae D. Don of the Fabales Bromhead (Angiosperm Phylogeny Group 2003). The subfamilial and tribal classification of Potter et al. (2007) is being used as the basis for treating Rosaceae in the Flora of North America project (volume 9, Rosales in part). Currently, no tribal name exists for *Lyonothamnus* (Pankhurst 2007; Reveal 2006). Therefore, I am proposing the creation of a tribe, Lyonothamneae, to accomodate *Lyonothamnus*.

Tribus **Lyonothamneae** Brouillet, tribus nov. Type: *Lyonothamnus* A. Gray, Proc. Amer. Acad. Arts 20:291. 1885.

Arbores inermes. *Folia* opposita, simplicia vel composita; stipulae caducae, liberae; venatio pinnata. *Flores* perigyni; epicalyx (1–)2–3-bracteolatus; hypanthium campanulatum; torus nullus; carpella 2(–3), distincta, libera, styli terminales, distincti; ovula 2–4 vel plura, fasciculata. *Fructus* folliculi aggregati, styli tarde cadentes. Numerus basicus chromosomatum $x = 9$.

Trees unarmed. **Leaves** opposite, simple or compound; stipules caducous, free; venation pinnate. **Flowers**

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perigynous; epicalyx of (1–)2–3 bractlets; hypanthium campanulate; torus none; carpels 2(–3), distinct, free, styles terminal, distinct; ovules 2–4 or more, clustered. **Fruits** aggregated follicles (follicetum), styles tardily falling. $x = 9$.

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THE TAXONOMY OF NORTH AMERICAN LOTI (FABACEAE: LOTEAE): NEW NAMES IN *ACMISPON* AND *HOSACKIA*

Luc Brouillet

Herbier Marie-Victorin
Institut de recherche en biologie végétale
Université de Montréal
4101 Sherbrooke St. E
Montreal, Quebec, CANADA H1X 2B2
luc.brouillet@umontreal.ca

ABSTRACT

Within the context of the preparation of the second edition of The Jepson Manual and of the treatment of the group for the Flora of North America, the author recognizes two genera within North American Loteae: *Hosackia* and *Acmispon* (including *Ottleya* and *Syrmatium*). New names are provided for varieties within *Hosackia*, and for species and varieties not previously included within *Acmispon*.

RESUMEN

En el contexto de la preparación de la segunda edición de "The Jepson Manual" y del tratamiento del grupo para la Flora of North America, el autor reconoce dos géneros en las Loteae norteamericanas: *Hosackia* y *Acmispon* (que incluye *Ottleya* y *Syrmatium*). Se aportan nuevos nombres para variedades de *Hosackia*, y para especies y variedades no incluidas previamente en *Acmispon*.

The taxonomy of *Lotus* s.l. (Fabaceae: Loteae) has been controversial, particularly with respect to the issue of including or excluding the North American species from the genus; Cullen (1959) and Sokoloff (1999, 2000) together provide a summary of the taxonomic history involved. Following Greene (1890), it became usual (though not unanimous) to treat North American species within *Lotus* s.l., as was done, among others, by Ottley (1923, 1944), Isely (1981, 1993), Barneby (1989), Arambarri (2000), and Stenglein et al. (2003). Traditionally, three subgenera have been recognized in North America: *Hosackia*, *Syrmatium*, and *Acmispon*, the latter subdivided into sections *Microlotus* and *Simpeteria*. In the last 10 years, however, morphological studies have shown that North American taxa were distinct from Eurasian *Lotus* s.s. Therefore, Sokoloff (1999, 2000a, b; Sokoloff & Lock 2005) proposed the recognition of four genera of North American *Loteae*: *Hosackia*, *Acmispon*, *Syrmatium*, and *Ottleya* (section *Simpeteria* segregated), corresponding with the four traditionally used subgeneric groups mentioned above. This taxonomy was accepted by Arambarri et al. (2005) in their numerical taxonomic study of the American species. The molecular phylogenetic analyses of Allan and Porter (2000) and Allan et al. (2003), based on the nrDNA internal transcribed spacer (ITS), confirmed that the North American taxa were distinct from *Lotus* s.s. and resulted in the recognition of two clades among American species: the *Hosackia* clade and the clade comprising the subgenera *Acmispon* and *Syrmatium*, and section *Simpeteria* (*Ottleya*), hereafter called the *Acmispon* clade. *Hosackia* appears monophyletic on both morphological (e.g., triaperturate pollen, leafy stipules) and molecular grounds, except for the unexplained position of *L. aboriginus* in Allan and Porter (2000). Nomenclatural transfer of some varieties recognized in *Hosackia* species has yet to be done, however.

The taxonomic disposition of species within the *Acmispon* clade (Allan & Porter 2000; Allan et al. 2003) (with 4-aperturate pollen and gland-like stipules, among others) appears less clear-cut. While there was some resolution within the clade in the ITS-based phylogenetic study of Alan and Porter (2000), Allan et al. (2003) showed a well-supported but unresolved *Acmispon* clade. In the Allan and Porter analysis, subgenus *Syrmatium* appears monophyletic, with *L. salsuginosus* (*Acmispon maritimus*, sect. *Acmispon*, Sokoloff 2000) – *L. aboriginus* (*Hosackia*) as sister to the subclade. A second subclade includes members of sections *Simpeteria* (*Ottleya*, Sokoloff 1999) and *Microlotus* (*L. wrangelianus*; *Acmispon* sect. *Anisolotus*, Sokoloff 2000). It is worth noting that Ottley (1944) included her new section *Simpeteria* within *Lotus* subgenus *Acmispon*.

Thus *Acmispon*, as defined by Sokoloff (2000) and as traditionally understood, appears polyphyletic in the ITS phylogeny, each section belonging to a separate clade. Only two members of *Acmispon* were included in the study, which prevents further conclusion. Thus, contrary to what morphological data may suggest, it does not seem possible to clearly delimit three monophyletic groups within the clade. Therefore, I am suggesting that two genera should be recognized among American Loti at the present time, corresponding to the two clades recognized in molecular analyses: *Hosackia* and *Acmispon* (the oldest generic name available for the *Acmispon* clade). Given the ambiguity concerning the monophyly of lineages within *Acmispon*, I prefer not to recognize subgeneric taxa at the present time, even though the *Syrmatium* group appears monophyletic. The delimitation of such taxa will have to be evaluated using more complete molecular and morphological data sets.

The purpose of this paper is to provide the nomenclatural combinations that are needed in *Hosackia* and *Acmispon*, particularly in view of the upcoming treatments of these genera for the second edition of The Jepson Manual and for the Flora of North America project. I am mainly following the taxonomy of Isely (1981, 1993) for the North American species. A list of already accepted names in *Hosackia* and *Acmispon* for North America north of Mexico is provided.

NEW COMBINATIONS IN *HOSACKIA*

Hosackia crassifolia Benth. var. **otayensis** (Moran ex Isely) Brouillet, comb. nov. Basionym: *Lotus crassifolius* (Benth.) Greene var. *otayensis* Moran ex Isely, Brittonia 30:466–467. 1978.

Hosackia oblongifolia Benth. var. **cuprea** (Greene) Brouillet, comb. nov. Basionym: *Lotus cupreus* Greene, Leafl. Bot. Obs. Crit. 1(5):74, 1904. *Hosackia cuprea* (Greene) Smiley, Univ. Calif. Publ. Bot. 9:257. 1921. *Lotus oblongifolius* (Benth.) Greene var. *cupreus* (Greene) Ottley, Univ. Calif. Publ. Bot. 10(3):206. 1923.

Hosackia stipularis Benth. var. **ottleyi** (Isely) Brouillet, comb. nov. Basionym: *Lotus stipularis* (Benth.) Greene var. *ottleyi* Isely, Brittonia 30:468–469. 1978.

NEW COMBINATIONS IN *ACMISPON*

Acmispon americanus (Nutt.) Rydb. var. **helleri** (Britton) Brouillet, comb. nov. Basionym: *Lotus helleri* Britton, Bull. Torrey Bot. Club 17:312–323. 1890. *Hosackia helleri* (Britton) Brand, Bot. Jahrb. Syst. 25:228. 1898. *Hosackia helleri* (Britton) Blomq. & Oosting, Spring Fl. Piedmont 79. 1940. *Acmispon helleri* (Britton) A. Heller, Cat. N. Amer. Pl. 205. 1914. *Acmispon helleri* (Britton) Small, Man. S.E. Fl. 687. 1933. *Lotus purshianus* Clem. & E.G. Clem. var. *helleri* (Britton) Isely, Brittonia 30:468. 1978. *Lotus unifoliolatus* Benth. var *helleri* (Britton) Kartesz & Gandhi, Phytologia 71:96. 1991.

Acmispon argophyllus (A. Gray) Brouillet, comb. nov. Basionym: *Hosackia argophylla* A. Gray, Pl. Nov. Thurb. 316. 1854. *Syrmatium argophyllum* (A. Gray) Greene, Bull. Calif. Acad. Sci. 2:147. 1886. *Lotus argophyllus* (A. Gray) Greene, Pittonia 2:149. 1890. *Acmispon argophyllus* (A. Gray) Brouillet var. *argophyllus*. *Hosackia argophylla* A. Gray var. *argophylla*.

Hosackia argentea Kellogg, Proc. Calif. Acad. Sci. 3:38. 1863.

Hosackia argophylla A. Gray var. *decora* I.M. Johnst., Bull. S. Calif. Acad. Sci. 17(2):63–64. 1918. *Lotus argophyllus* (A. Gray) Greene var. *decorus* (I.M. Johnst.) Ottley, Univ. Calif. Publ. Bot. 10(3):237–238. 1923. *Lotus argophyllus* (A. Gray) Greene subsp. *decorus* (I.M. Johnst.) Munz, Fl. S. Calif. 446. 1974.

Acmispon argophyllus (A. Gray) Brouillet var. **adsurgens** (Dunkle) Brouillet, comb. nov. Basionym: *Lotus argophyllus* (A. Gray) Greene var. *adsurgens* Dunkle, Bull. S. Calif. Acad. Sci. 39:197. 1941. *Lotus argophyllus* (A. Gray) Greene subsp. *adsurgens* (Dunkle) P.H. Raven, Aliso 5:326. 1963.

Acmispon argophyllus (A. Gray) Brouillet var. **argenteus** (Dunkle) Brouillet, comb. nov. Basionym: *Lotus argophyllus* (A. Gray) Greene var. *argenteus* Dunkle, Bull. S. Calif. Acad. Sci. 39:176. 1940.

Hosackia ornithopus Greene, Bull. Calif. Acad. Sci. 1:185. 1885. *Syrmatium ornithopus* (Greene) Greene, Bull. Calif. Acad. Sci. 2:148. 1886. *Lotus ornithopus* (Greene) Greene, Pittonia 2:149. 1890. *Lotus argophyllus* (A. Gray) Greene var. *ornithopus* (Greene) Ottley, Univ. Calif. Publ. Bot. 10:238. 1923. *Lotus argophyllus* subsp. *ornithopus* (Greene) P.H. Raven, Aliso 5:326. 1963.

Lotus argophyllus (A. Gray) Greene var. *hancockii* Dunkle, Bull. S. Calif. Acad. Sci. 39:175. 1940.

Hosackia venusta Eastw., Proc. Calif. Acad. Sci., Ser. 3, 1:103, t. 8. 1898. *Hosackia ornithopus* Greene subsp. *venusta* (Eastw.) Abrams, Ill. Fl. Pac. States 2:550. 1944. *Lotus venustus* (Eastw.) A. Heller, Cat. N. Amer. Pl. 7. 1900. *Syrmatium venustum* (Eastw.) Davidson & Moxley, Fl. S. Calif. 199. 1923.

Acmispon argophyllus (A. Gray) Brouillet var. **fremontii** (A. Gray) Brouillet, comb. nov. Basionym: *Hosackia argophylla* A. Gray var. *fremontii* A. Gray, Proc. Acad. Nat. Sci. Philadelphia 15:347. 1864. *Hosackia fremontii* (A. Gray) Abrams, Ill. Fl. Pacific States 2:550. 1944. *Lotus fremontii* (A. Gray) A. Heller, Cat. N. Amer. Pl. 7. 1900. *Syrmatium fremontii* (A. Gray) A. Heller, Muhlenbergia 9(5):67. 1913. *Lotus argophyllus* (A. Gray) Greene var. *fremontii* (A. Gray) Ottley, Univ. Calif. Publ. Bot. 10(3):237–238. 1923.

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Acmispon argyreus (Greene) Brouillet, comb. nov. Basionym: *Hosackia argyraea* Greene, Bull. Calif. Acad. Sci. 1(4A):184. 1886 [1885]. *Lotus argyraeus* (Greene) Greene, Pittonia 2:144. 1890. *Anisolotus argyraeus* (Greene) A. Heller, Muhlenbergia 8:47. 1912. *Ottleya argyraea* (Greene) D.D. Sokoloff, Feddes Repert. 110 (1–2):94.

Acmispon argyraeus (Greene) Brouillet var. **multicaulis** (Ottley) Brouillet, comb. nov. Basionym: *Lotus wrightii* (A. Gray) Greene var. *multicaulis* Ottley, Univ. Calif. Publ. Bot. 10:211, pl. 70. 1923. *Hosackia wrightii* A. Gray subsp. *multicaulis* (A. M. Ottley) Abrams, Ill. Fl. Pac. States 2:543. 1944. *Lotus argyraeus* (Greene) Greene subsp. *multicaulis* (Ottley) Munz, Aliso 4:93. 1958. *Lotus argyraeus* (Greene) Greene var. *multicaulis* (Ottley) Isely, Brittonia 30:466. 1978.

Acmispon argyraeus (Greene) Brouillet var. **notitius** (Isely) Brouillet, comb. nov. Basionym: *Lotus argyraeus* (Greene) Greene var. *notitius* Isely, Brittonia 30:466. 1978.

Acmispon cytisoides (Benth.) Brouillet, comb. nov. Basionym: *Hosackia cytisoides* Benth., Trans. Lin. Soc. London 17:366. 1837, non *Lotus cytisoides* L. 1753. *Syrmatium cytisoides* (Benth.) Greene, Bull. Calif. Acad. Sci. 2:147. 1886.

Hosackia cytisoides Benth. var. *rubescens* Nutt. ex Torr. & A. Gray, Fl. N. Amer. 1(2):324. 1838. *Hosackia rubescens* (Torr. & A. Gray) Anon., in index., Proc. Biol. Soc. Wash. 13:203. 1900. *Depranolobus rubescens* Nutt. ex Torr. & A. Gray, Fl. N. Amer. 1(2):324. 1838.

Lotus benthamii Greene, Pittonia 2(9):148. 1890.

Acmispon dendroideus (Greene) Brouillet, comb. nov. Basionym: *Syrmatium dendroideum* Greene, Bull. Calif. Acad. Sci. 2(6B):146. 1886. *Lotus dendroideus* (Greene) Greene, Pittonia 2:148. 1890. *Hosackia dendroidea* (Greene) Abrams, Ill. Fl. Pacific States 2:552. 1944.

Acmispon dendroideus (Greene) Brouillet var. **traskiae** (Noddin) Brouillet, comb. nov. Basionym: *Syrmatium traskiae* Eastw. ex Noddin Fl. Los Ang. 201. 1917. *Lotus scoparius* (Nutt. ex Torr. & A. Gray) Ottley var. *traskiae* (Eastw. ex Noddin) Ottley, Univ. Calif. Publ. Bot. 10(3):229. 1923. *Lotus scoparius* (Nutt. ex Torr. & A. Gray) Ottley subsp. *traskiae* (Noddin) P.H. Raven, Aliso 5:326. 1963. *Lotus dendroideus* (Greene) Greene var. *traskiae* (Noddin) Isely, Brittonia 30:467. 1978.

Acmispon dendroideus (Greene) Brouillet var. **veatchii** (Greene) Brouillet, comb. nov. Basionym: *Hosackia veatchii* Greene, Bull. Calif. Acad. Sci. 1:83. 1885. *Syrmatium veatchii* (Greene) Greene, Bull. Calif. Acad. Sci. 2:148. 1886. *Lotus veatchii* (Greene) Greene, Pittonia 2:148. 1890. *Lotus scoparius* (Nutt. ex Torr. & A. Gray) Ottley var. *veatchii* (Greene) Ottley, Univ. Calif. Publ. Bot. 10(3):228. 1923. *Lotus dendroideus* (Greene) Greene var. *veatchii* (Greene) Isely, Brittonia 30:467. 1978.

Syrmatium patens Greene, Bull. Calif. Acad. Sci. 2:147. 1886.

Acmispon distichum (Greene) Brouillet, comb. nov. Basionym: *Hosackia disticha* Greene, Bull. Calif. Acad. Sci. 1(4A):186. 1885. *Syrmatium distichum* (Greene) Greene, Bull. Calif. Acad. Sci. 2(6B):148. 1886. *Lotus distichus* (Greene) Greene, Pittonia 2(9):149. 1890.

Acmispon flexuosus (Greene) Brouillet, comb. nov. Basionym: *Hosackia flexuosa* Greene, Bull. Calif. Acad. Sci. 1:82. 1885, non *Lotus flexuosus* Desr. 1792. *Ottleya flexuosa* (Greene) D.D. Sokoloff, Feddes Repert. 110(1–2):94. 1999.

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Acmispon glabrus (Vogel) Brouillet, comb. nov. Basionym: *Syrmatium glabrum* Vogel, Linnaea 10:591. 1835–1836. *Lotus glaber* (Vogel) Greene, Pittonia 2:148. 1890, nom. illeg., non *Lotus glaber* Mill. 1768. *Hosackia glabra* (Vogel) Torr., U. S. Expl. Exped., Phan. 2:274. 1874. *Hosackia crassifolia* Nutt. ex Torr. & A. Gray subsp. *glabra*. *Anisolotus glaber* (Vogel) M. Armstr. & Thornber, Field Book W. Wild Fl. 244. 1915.

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Acmispon glabrus (Vogel) Brouillet var. **brevialatus** (Ottley) Brouillet, comb. nov. Basionym: *Lotus scoparius* (Nutt. ex Torr. & A. Gray) Ottley var. *brevialatus* Ottley, Univ. Calif. Publ. Bot. 10(3):227, pl. 77, fig. 10–16. 1923. *Hosackia glabra* (Vogel) Torr. subsp. *brevialata* (A. M. Ottley) Abrams, Ill. Fl. Pacific States 2:552. 1944. *Lotus scoparius* (Nutt. ex Torr. & A. Gray) Ottley subsp. *brevialatus* (Ottley) Munz, Fl. S. Calif. 450. 1974.

Acmispon grandiflorus (Benth.) Brouillet, comb. nov. Basionym: *Hosackia grandiflora* Benth., Trans. Linn. Soc. London 17:366. 1837. *Lotus grandiflorus* (Benth.) Greene, Pittonia 2:145. 1890. *Anisolotus grandiflorus* (Benth.) A. Heller, Mulhenbergia 8(1–2):20. 1912. *Ottleya grandiflora* (Benth.) D.D. Sokoloff, Feddes Repert.110(1–2):94. 1999.

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Lotus leucophaeus Greene, Pittonia 2:145. 1890. *Anisolotus leucophaeus* (Greene) A. Heller, Mulhenbergia 8:48. 1912. *Hosackia leucophaea* (Greene) Abrams, Ill. Fl. Pacific States 2:542. 1944.

Lotus confinis Greene, Erythea 1(12):258. 1893.

Lotus grandiflorus (Benth.) Greene var. *mutabilis* Ottley, Univ. Calif. Publ. Bot. 10(3):208, pl. 68, fig. 2–6, pl. 69, fig. 1. 1923.

Acmispon grandiflorus (Benth.) Brouillet var. **macranthus** (Greene) Brouillet, comb. nov. Basionym: *Lotus grandiflorus* (Benth.) Greene var. *macranthus* (Greene) Isely, Brittonia 30:467. 1978. *Hosackia macrantha* Greene, Bull. Calif. Acad. Sci. 1:81. 1885. *Lotus macranthus* (Greene) Greene, Pittonia 2(9):146. 1890. *Anisolotus macranthus* (Greene) A. Heller, Mulhenbergia 8(4):48. 1912.

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Hosackia mollis Greene, Bull. Calif. Acad. Sci. 1:185. 1885, nom. illeg., non Nutt. 1838. *Anisolotus mollis* (Greene) A. Heller, Muhlenbergia 8:60. 1912. *Lotus mollis* (Greene) Greene, Pittonia 2:143. 1890, non Balf. f. 1882. *Lotus greenei* Ottley, J. Wash. Acad. Sci. 29(11):483. 1939, nom. nov.

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Acmispon haydonii (Orcutt) Brouillet, comb. nov. Basionym: *Hosackia haydonii* W. Amer. Sci. 6:63. 1889. *Lotus haydonii* (Orcutt) Greene, Pittonia 2(9):149. 1890. *Syrmatium haydonii* (Orcutt) Brand, Bot. Jahrb. Syst. 25:228. 1898. *Syrmatium haydonii* (Orcutt) A. Heller, Muhlenbergia 9(5):67. 1913.

Acmispon heermannii (Greene) Brouillet, comb. nov. Basionym: *Hosackia heermannii* Durand & Hilg., Pl. Heermann. 39. 1854. *Syrmatium heermannii* (Durand & Hilg.) Greene, Bull. Calif. Acad. Sci.2(6B):148. 1886. *Lotus heermannii* (Durand & Hilg.) Greene, Pittonia 2(9):150. 1890. *Lotus eriophorus* Greene var. *heermannii* (Durand & Hilg.) Ottley, Univ. Calif. Publ. Bot. 10(3):232–234. 1923.

Hosackia decumbens Benth. var. *glabriuscula* Hook. & Arn., Bot. Beechey Voy. 137. 1832. *Hosackia tomentosa* Hook. & Arn. subsp. *glabriuscula* (Hook. & Arn.) Abrams, Ill. Fl. Pacific States 2:546. 1944.

Acmispon heermannii (Greene) Brouillet var. **orbicularis** (A. Gray) Brouillet, comb. nov. Basionym: *Hosackia heermannii* Durand & Hilg. var. *orbicularis* A. Gray, Proc. Acad. Nat. Sci. Philadelphia 15:348. 1864. *Lotus heermannii* (Durand & Hilg.) Greene var. *orbicularis* (A. Gray) Isely, Brittonia 30:467. 1978.

Lotus eriophorus Greene, Erythea 1(10):207. 1893. *Lotus heermannii* (Durand & Hilg.) Greene var. *eriophorus* (Greene) Ottley, Brittonia 5:81. 1944. *Syrmatium eriophorum* (Greene) A. Heller, Muhlenbergia 9(5):67. 1913.

Hosackia tomentosa Hook. & Arn., Bot. Beechey Voy. 137. 1832. *Hosackia tomentosa* Hook. & Arn. subsp. *tomentosa*. *Lotus tomentosus* (Hook. & Arn.) Greene, Pittonia 2:150. 1890, nom. illeg., non Desr. 1792. *Syrmatium tomentosum* (Hook. & Arn.) Vogel, Linnaea 10:591. 1835–36.

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MICRANTHES NELSONIANA VAR. *PORSILDIANA* (SAXIFRAGACEAE), THE PROPER NAME AT THE VARIETAL LEVEL

Luc Brouillet

Herbier Marie-Victorin
Institut de recherche en biologie végétale
Université de Montréal
4101 rue Sherbrooke E
Montréal, Quebec, CANADA H1X 2B2
luc.brouillet@umontreal.ca

ABSTRACT

When the two entities are merged, the name **Micranthes nelsoniana** var. **porsildiana** has priority over var. *pacifica*. A new combination is therefore presented. Furthermore, the combination *M. petiolaris* (Raf.) Bush is considered valid.

RESUMEN

Cuando se unen las dos entidades, el nombre **Micranthes nelsoniana** var. **porsildiana** tiene prioridad sobre var. *pacifica*. Por ello se presenta una nueva combinación. Además, la combinación *M. petiolaris* (Raf.) Bush se considera válida.

Micranthes nelsoniana

Recently, Brouillet and Gornall (2007) presented new combinations in *Micranthes* for the North American flora. In the treatment of the genus for the Flora of North America, Elvander and Brouillet (ined.) are merging two infraspecific taxa of *Micranthes nelsoniana* (D. Don) Small that had traditionally been considered distinct: varieties or subspecies *pacifica* and *porsildiana*. Subspecific and varietal names exist for both entities in *Saxifraga*. When merging the taxa at the subspecific level, the name *pacifica* has priority over *porsildiana*. At the varietal level, however, *porsildiana* has priority over *pacifica* (see taxonomy below). Currently, the varietal level is being used for the Flora of North America treatment. In publishing new names, however, Brouillet and Gornall (loc. cit.) made a combination for var. *pacifica* but not for var. *porsildiana*. A new combination in *Micranthes* for the latter is therefore required and is presented here. Since Gornall and Ohba (ined.) had prepared combinations for all varieties in *Micranthes nelsoniana*, I am attributing the new combination to these authors.

Micranthes nelsoniana (D. Don) Small var. **porsildiana** (Calder & Savile) Gornall & H. Ohba, comb. nov.
Basionym: *Saxifraga punctata* L. subsp. *porsildiana* Calder & Savile, Canad. J. Bot. 38:429. 1960. *Saxifraga punctata* var. *porsildiana* (Calder & Savile) B. Boivin, Naturaliste Canad. 93:646. 1966. *Saxifraga nelsoniana* D. Don subsp. *porsildiana* (Calder & Savile) Hultén, Not. Bot. 126:494. 1973. *Saxifraga nelsoniana* var. *porsildiana* (Calder & Savile) H. Ohba, J. Jap. Bot. 68:336. 1993.

Micranthes nelsoniana (D. Don) Small var. *pacifica* (Hultén) Gornall & H. Ohba, J. Bot. Res. Inst. Texas 1:1020. 2007. *Saxifraga punctata* L. subsp. *pacifica* Hultén, Acta Univ. Lund. n.s. 41:928. 1945. *Saxifraga nelsoniana* D. Don subsp. *pacifica* (Hultén) Hultén. *Saxifraga nelsoniana* var. *pacifica* (Hultén) H. Ohba, J. Jap. Bot. 68:336. 1993.

Micranthes petiolaris

Brouillet and Gornall (2007) made a new combination for *Micranthes petiolaris*. The combination by Bush (1928), however, is currently considered valid and has priority. Therefore, *Micranthes petiolaris* (Raf.) Brouillet & Gornall must be considered an isonym.

Micranthes petiolaris (Raf.) Bush, Amer. Midl. Naturalist 11:225. 1928. Basionym: *Hexaphoma petiolaris* Raf., Fl. Tellur. 2:67. 1837. *Saxifraga michauxii* Britton ex Small & Vail, Mem. Torrey Bot. Club 4:118. 1894. *Micranthes petiolaris* (Raf.) Brouillet & Gornall, J. Bot. Res. Inst. Texas 1:1021. 2007.

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NOMENCLATURAL CHANGES IN *NEMACLADUS* (CAMPANULACEAE)

Nancy R. Morin[1]

Biology Department
Northern Arizona University
Flagstaff, Arizona 86011, U.S.A.

ABSTRACT

Based on morphological and DNA sequence evidence, *Parishella californica* is transferred to *Nemacladus*, and *Nemacladus glanduliferus* var. *orientalis*, *Nemacladus glanduliferus* var. *australis*, and *Nemacladus rubescens* var. *tenuis* are recognized as species. Two new varieties and one new species are named: **Nemacladus tenuis** var. **aliformis, Nemacladus secundiflorus** var. **robbinsii,** and **Nemacladus calcaratus.**

RESUMEN

Basados en pruebas morfológicas y secuencias DNA, *Parishella californica* se transfiere a *Nemacladus*, y *Nemacladus glanduliferus* var. *orientalis*, *Nemacladus glanduliferus* var. *australis*, y *Nemacladus rubescens* var. *tenuis* se reconocen como especies. Se nombran dos nuevas variedades y una nueva especie: ***Nemacladus tenuis*** var. ***aliformis***, ***Nemacladus secundiflorus*** var. ***robbinsii***, y **Nemacladus calcaratus.**

Nemacladus is an isolated genus in Campanulaceae (Nemacladoideae M.H.G. Gustafsson, Lammers 2007a, 2007b, or Nemacladaceae Nuttall, Takhtajan 1997, which include *Pseudonemacladus* McVaugh and *Parishella* A. Gray) basal to the Campanuloideae and Lobelioideae (Cosner et al. 1994) or sister to a clade comprising Cyphiaceae, Cyphocarpaceae, and Lobeliaceae (Gustafsson & Bremer 1995). Distributed in southwestern U.S. and northern Mexico, extending south to Sonora and Baja California and north into southeastern Oregon and western Wyoming, it is most diverse in California. Filaments connate for part of their length distinguish it from Campanuloideae, free anthers distinguish it from Lobelioideae, and absence of a fluid filled cavity in the stigma separates it from Cyphioideae.

A detailed study of *Nemacladus* has been in progress since the author prepared a treatment of it for the Jepson Manual (Morin & Milburn 1993). Extensive field work, study of herbarium specimens, and, in collaboration with T.J. Ayers at Northern Arizona University, analysis of DNA and study of floral and seed morphology using SEM, have been done for a monograph that is in preparation. In order to reflect the results of this work in the revision of the Jepson Manual in preparation, it is necessary to make some nomenclatural changes in advance of the full monograph.

The monospecific *Parishella* A. Gray, found in the Mojave Desert and disjunct in mountains in Santa Barbara County, California, has long been thought to be the genus most closely related to *Nemacladus* and is here transferred into *Nemacladus*. In ITS (Haberle 1998), and atpB (Ayers in prep.) analysis *Parishella californica* is nested within *Nemacladus*, with closest alliance to *N. rigidus* Curran. As in other *Nemacladus*, large, clear cells are attached to the filaments; the non-resupinate, nearly actinomorphic flowers with white, cup-shaped corolla are similar to those of *N. pinnatifidus* Greene.

Nemacladus californicus (A. Gray) Morin, comb. nov. *Parishella californicus* A. Gray, Bot. Gaz. 7:94. 1882. Type: CALIFORNIA. San Bernardino Co.: Rabbit Springs, Mohave Desert, *Parish 1328*, May 1882 (holotype: GH! isotypes: MO!, NY!, UC!).

McVaugh (1939) recognized three varieties in *N. glanduliferus* based on their habit and the aspect of the pedicels, considering the flowers to be similar in all three. The flowers differ significantly, however, and these taxa are here recognized as species. *Nemacladus glanduliferus* and *N. orientalis* are sister taxa in the atpB and ITS analysis (Ayers, in prep.).

Nemacladus glanduliferus Jepson has nearly actinomorphic, upward facing flowers that are mostly resupinate, petals white, all similar in size and shape, connate at base forming a cuplike tube, free lobes reflexed;

[1]Contact address, Nancy R. Morin, P.O. Box 716 Point Arena, California 95468, U.S.A.

filament tube and style erect, arching over flower; capsule hemispheric with base and apex rounded, 2–2.3 mm diameter. It occurs in desert areas of California, Arizona, and northern Baja California and Sonora, Mexico.

Nemacladus orientalis has highly zygomorphic, outward-facing flowers that are not resupinate, petals white with maroon and sometimes yellow markings, free nearly to base, lower two petals longer and narrower than upper three petals; filament tube and style deflexed between lower two petals; capsules hemispheric with base rounded and apex acute, 1.5–2 mm diameter. It is widely distributed in desert areas of California, Nevada, Arizona, Utah, north to Wyoming and south to Baja California and Sonora, Mexico.

Nemacladus australis has highly zygomorphic, outward-facing flowers that are not resupinate, petals white with maroon markings, free nearly to base, lower two petals longer and narrower than upper three petals, filament tube and style deflexed between lower two petals; capsules spherical, 3.5–4 mm diameter. It is known from Rosario, Bajia de los Angelos, Santa Catarina, El Terminal, and Sierra Calvario, in Baja California.

Nemacladus orientalis (McVaugh) Morin, comb. et stat. nov. *Nemacladus glanduliferus* var. *orientalis* McVaugh, Amer. Midl. Naturalist 22: 540. 1939. Type: NEVADA. Clark Co.: shore of Lake Mead, near Boulder Dam, 2 May 1938, *Percy Train 1566* (holotype: NA-no. 52430; isotype: UNLV!).

Nemacladus australis (Munz) Morin, comb. et stat. nov. *Nemacladus rigidus* var. *australis* Munz, Amer. J. Bot. 11:242, tab. 10. 192. Type: BAJA CALIFORNIA. Rosario, 1 May 1886, *C.R. Orcutt 1348* (holotype: GH!; isotypes: MO!, UC!).

Nemacladus glanduliferus var. *australis* (Munz) McVaugh, Amer. Midl. Naturalist 22:540. 1939

Nemacladus rubescens Greene is one of the most striking species in the genus, with highly zygomorphic flowers and conspicuous markings on the petals. McVaugh named var. *tenuis* based on shape, size, and margins of the basal leaves, size of anthers, and nature of the clear cells attached to the filaments. Except for these characters, he believed the flowers were basically the same as typical *rubescens*. Field studies show that the flowers of *tenuis* are very different from those of *rubescens* and in ways that almost certainly preclude gene transfer between the two, and that there are two different floral mophologies within *tenuis*. *Nemacladus tenuis* is here recognized as a species with two varieties.

Nemacladus rubescens and *Nemacladus tenuis* both have silvery grey stems or reddish stems with a silvery sheen, and yellowish green leaves. *Nemacladus rubescens* has oblanceolate to elliptic, mostly obtuse leaves with entire margins; flowers face outward, are highly zygomorphic, not resupinate, petals divided nearly to base, yellowish with maroon markings, elliptic to lanceolate and straight; filament tube and style declined between two lower petals. *Nemacladus tenuis* has leaves oblanceolate, deeply pinnatifid; flowers face upward or outward, are resupinate, petals yellowish with maroon and yellow markings or white with pinkish or yellowish markings, lower three petals connate at base or divided nearly to base, together bowl-shaped; filament tube and style erect and arching over the flower.

Nemacladus tenuis (McVaugh) Morin, comb. et stat. nov. *Nemacladus rubescens* var. *tenuis* McVaugh, Amer. Midl. Naturalist 22: 536. 1939. Type: CALIFORNIA. Riverside Co.: E base of Indio Mt., Colorado Desert, 17 Apr 1905, *H.M. Hall 5819* (holotype: US 614929!; isotypes: ARIZ!, DS!, GH!, MO!, NY!, OSU!, P!, POM!, UC!).

Nemacladus tenuis var. **tenuis**

Sepals 0.7–1 mm long, linear; corolla divided 1/2 length, lobes nearly alike; all lobes white with deep pink or yellowish tips, deltate, 0.9–2 mm long; filaments 1–2 mm long, arched, anthers 0.4–0.5 mm long. Mojave and Sonoran Deserts.

Nemacladus tenuis var. **aliformis** Morin, var. nov. Type: CALIFORNIA. San Bernardino Co.: 1 mi E of junction with Hwy. 127 on Old Spanish Gentry Road, 26 Apr 2003, *Morin 589b* (holotype: ASC!).

A *Nemacladus tenuis* (McVaugh) Morin var. *tenuis* sepala anguste deltatus, 2 petalis summa castaneus, angustatus, arcuatus , filis longius, et antherae 0.5–0.6 mm longus differt.

Sepals 1–2.5 mm long, narrowly deltate; corolla divided nearly to base, 2 upper lobes maroon or brownish, linear, arched, 0.9–2.5 × 0.3–0.5 mm long, 3 lower lobes white with yellow and brownish marks, 0.9–2.2 mm long, ciliate; filaments 2–3.5 mm long, anthers 0.5–0.6 mm long. Mohave Desert.

Etymology.—The epithet "aliformis" (from ala, wing, and -formis, with the form of) refers to the winged appearance of the flowers, which resemble small flying insects.

Robbins (1958) helped clarify the circumscription of *Nemacladus* species that have resupinate flowers with corollas that are mostly white or white with a lilac or pink tinge. One of these is *Nemacladus secundiflorus* G.T. Robbins, known from the South Coast Ranges and Greenhorn Mountains in California. He noted an unusual population (*Raven 9138* and *Bacigalupi 5649*) from San Benito County but concluded it was not different enough to warrant recognition. Study of fresh material and additional populations indicates that the flowers of these plants consistently differ from typical *secundiflorus* in being much smaller and in having a narrower corolla tube.

Nemacladus secundiflorus var. *secundiflorus* has flowers with a white corolla, sometimes with pinkish veins, tube 2.5–3.5 mm long, broadly cylindrical, upper 2 lobes widely spreading, 2–2.5 mm long, glabrous to hairy, lower lobes reflexed, 2.5–3 mm long; filaments ± 2–2.5 mm long, anthers 0.5–0.7 mm long, with many long, ca. 0.7 mm hairs. South Coast Ranges in Monterey and San Luis Obispo counties, and the Greenhorn Mountains in Tulare and Kern counties.

Nemacladus secundiflorus var. **robbinsii** Morin, var. nov. Type: CALIFORNIA. San Benito Co.: just W of the junction to Pinnacles on the road from Hollister to Bitterwater, 5 May 1956, *Raven, Stebbins, et al., 9138* (holotype: JEPS 14554! isotypes: DS!, JEPS 78490!, NY!, RSA!, SBBG!, SLO!, US!).

A *Nemacladus secundiflorus* Robbins var. *secundiflorus* flores parvioribus , corollae tubus 0.5–0.8 mm longus, lobis 0.3–0.5 mm longus, antherae 0.1 mm longus differt.

Corolla white or pale lavender; tube 0.5–0.8 mm long, narrowly cylindrical, upper 2 lobes spreading, 0.3–0.5 mm long, glabrous, lower lobes reflexed, 0.3–0.5 mm long; filaments ± 0.8 mm long, anthers 0.1 mm long, hairs absent or few, ca. 0.5 mm long. South Coast Ranges in San Benito, San Luis Obispo, and Ventura counties with one population in the Greenhorn Mountains in Tulare Co.

Etymology.—Variety *robbinsii* is named in honor of Guy Thomas Robbins, 1916–1960, in recognition of his careful and perceptive studies of *Nemacladus*. He received a B.S. from the University of California, Berkeley and an M.S. at University of Colorado, Boulder, after which he was on the faculty at University of Arizona and at Oklahoma State College, Ada. He then entered the Ph.D program at University of California, Berkeley and in 1952 took a full-time position as a Research Botanist in the Jepson Herbarium. In addition to his work on *Nemacladus*, he published a revision of North American *Androsace* (Robbins 1944). Additional information about his life can be found in the memoirs of Lavinia Pearl Butler Robbins (1882–1985), his mother, who donated her memoirs in 1972 to the Bancroft Library at University of California, Berkeley, in his memory.

Nemacladus calcaratus Morin, sp. nov. Type: CALIFORNIA. Tulare Co.: S of Chimney Creek Campground, ca. 9.3 air mi W of Hwy 395, sandy flats between granitic boulders, near 35.83N, 118.04W, 1745 m, 4 Jun 2008, *Morin 641* (holotype: ASC!; isotype: UC!).

Species corollae calcaratus a congeneribus diversa.

Plants 2–4 cm tall, branched from base or 0.5–1 cm from base, axis somewhat zig-zagged, stems widely spreading at a 60–75° angle to axis, sparsely hairy; internodes 0.5–1 cm. Basal leaves green with reddish margins, narrowly lanceolate to spatulate, 2–5 × 0.2–1.5 mm, remotely toothed, densely hairy, apex acute. Bracts 1–1.2(–2) mm long, ovate-lanceolate, entire or remotely and minutely toothed, sparsely hairy, ± clasping pedicel at base, abruptly arched away from pedicel 1/3 to 1/2 from base, apex minutely apiculate; pedicels straight or arched, 1–1.2 cm long, ± densely hairy at base, more sparsely hairy distally. Flowers bilaterally symmetrical, not resupinate; hypanthium tube hemispheric to broadly obconic, ca. 0.5 mm long; calyx lobes lanceolate, glabrous, lowest calyx lobe reflexed and appressed at base to spur, 1.2–1.5 × 0.5 mm, 2 flanking lobes 1.2–1.5 mm long, upper 2 lobes 0.8–1 mm long; petals radiating on adaxial (upper) side of corolla, white with longitudinal red or maroon line on proximal half, ovate, apex acute, bearing slender,

0.4 mm, downward pointing hairs abaxially and adaxially, lowest 2 petals connate basally 1 mm forming a spur, free portion 2.5 × 1.5 mm, 2 flanking and uppermost petals narrower, ca. 2.5 × 1 mm; filaments connate in distal 2/3, 1.8–2 mm, bearing 0.5–1 mm long hairs at apex, 2 narrow, yellow, stipe-like appendages extending from near base of filaments terminated by semicircular pad from which 8–12 clear, narrow, acute cells ca. 0.3 mm long radiate, anthers 0.3–0.4 mm; ovary subinferior, broadly hemispheric, base obtuse, apex nearly flat, 3 glands alternating with filaments low, oblong, densely papillate; capsule ca. 3 mm long, calyx lobes splayed outward.

Nemacladus calcaratus is known only from the Chimney Creek area, Tulare County, California at the southern end of the Pacific Crest.

Etymology.—*Calcaratus* is in reference to the nectar spur. Ertter et al. (*6331*) noted the red stripes on the corolla, and Boyd and Bramlet (*1931*) pointed out the small spur. It is the first species of *Nemacladus* known to have a definite nectar spur, although the corolla of *Nemacladus ramosissimus* Nutt. is gibbous. The flat ovary apex and relatively large corolla with all petals arranged on the upper part are also distinctive.

Other specimens seen: **CALIFORNIA. Tulare Co.:** 24 air mi ENE Kernville, ridge S of Chimney Creek Campground, at W end of ridge, elev. 6200 ft, 9 Jun 1986, *Ertter, Holland, and Dains 6331* (RSA, UC); Southern Sierra Nevada, Chimney Creek Canyon, north Slope Peak 7155, south Chimney Meadow, elev. 6800 ft, 9 Jun 1986, *Boyd & Bramlet 1931* (CAS, RSA).

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PHYLOGENETIC ANALYSIS OF NORTH AMERICAN PLUMS (*PRUNUS* SECT. *PRUNOCERASUS*: ROSACEAE) BASED ON NUCLEAR *LEAFY* AND *S6PDH* SEQUENCES

Joseph R. Rohrer,[1] Megan A. O'Brien, and Julie A. Anderson

Department of Biology
University of Wisconsin-Eau Claire
Eau Claire, Wisconsin 54702-4004, U.S.A.

ABSTRACT

Phylogenetic analysis of DNA sequences from two low-copy nuclear genes (*LEAFY* and *s6pdh*) was conducted to investigate relationships among native plums of North America (*Prunus* sect. *Prunocerasus*). The cladograms resulting from maximum parsimony and Bayesian inference are poorly resolved and incongruent with clades based on chloroplast DNA sequences. Evidence from both nuclear genes confirms the placement of *P. texana* in sect. *Prunocerasus*. Sequences of *P. americana* and *P. mexicana* form a monophyletic group on the *s6pdh* cladogram, but most *P. americana* collections also have a second divergent sequence, which together form a clade sister to *P. subcordata*. The shared possession of a 250-bp insertion within *LEAFY* intron 2 supports a close relationship between *P. hortulana* and *P. murrayana*. *Prunus alleghaniensis, P. gracilis, P. maritima,* and *P. umbellata* form a paraphyletic group on the *LEAFY* cladogram, basal to a clade composed of *P. angustifolia* and *angustifolia*-like sequences of *P. rivularis* and *P. munsoniana*. Data from *LEAFY* and *s6pdh* suggest hybrid origins for *P. rivularis* and *P. munsoniana*, with *P. angustifolia* as one progenitor.

RESUMEN

Se realizó un análisis filogenético de secuencias de DNA de dos genes nucleares (*LEAFY* y *s6pdh*) para investigar las relaciones entre los ciruelos nativos de Norte América (*Prunus* sect. *Prunocerasus*). Los cladogramas que resultan de la máxima parsimonia e inferencia bayesiana tienen una resolución pobre y son incongruentes con clados basados en secuencias de DNA plastidial. Los resultados de ambos genes nucleares confirman la colocación de *P. texana* en la sect. *Prunocerasus*. Las secuencias de *P. americana* y *P. mexicana* forman un grupo monofilético en el cladograma de *s6pdh*, pero la mayor parte de las colecciones de *P. americana* tienen una segunda secuencia divergente, que juntas forman un clado hermano de *P. subcordata*. La posesión compartida de una inserción de 250-bp en el intrón 2 de *LEAFY* apoya una relación fuerte entre *P. hortulana P. murrayana*. *Prunus alleghaniensis, P. gracilis, P. maritima,* y *P. umbellata* forman un grupo parafilético en el cladograma de *LEAFY*, basal al clado compuesto por *P. angustifolia* y secuencias similares a *angustifolia* de *P. rivularis* y *P. munsoniana*. Los datoa de *LEAFY* y *s6pdh* sugieren origen híbrido para *P. rivularis* y *P. munsoniana*, con *P. angustifolia* como uno de los progenitores.

INTRODUCTION

Prunus is one of the larger genera of the Rosaceae with about 200 species, which are most abundant in the North Temperate zone but also range into the tropics and Southern Hemisphere (Rehder 1940; Robertson 1974). It is important commercially as the source of cherries, almonds, peaches, nectarines, apricots, and plums; numerous species are grown ornamentally for their beautiful early-spring flowers. The classification of *Prunus* has been debated from Linnaeus to the present day, with some botanists arguing for a broad concept of the genus that includes all of the fruits mentioned above (e.g., McVaugh 1951; Robertson 1974) and others dividing *Prunus* into a variety of segregate genera including *Amygdalus, Armeniaca, Cerasus, Laurocerasus, Padus,* and *Persica* (e.g., Iwatsuki et al. 2001; Flora of China Editorial Committee 2003). The most widely used classification has been that of Rehder (1940) who recognized *Prunus* in its broad sense with five subgenera.

At the species level there has been considerable taxonomic uncertainty among the North American plums (*Prunus* sect. *Prunocerasus*). In 1892 Bailey called *Prunocerasus* the "hardest puzzle in American pomology," a memorable phrase quoted by Shaw and Small (2004) more than a century later in reporting the use of multiple cpDNA sequences to bear on this enduring puzzle. Shaw and Small (2004) provided an

[1]**Author for correspondence; email: jrohrer@uwec.edu**

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extensive review and analysis of the taxonomic history of *Prunocerasus*, and they noted that the unresolved classification of North American plums is the result of interspecific similarities, intraspecific variation, and probably interspecific hybridization.

The earliest studies using DNA sequences to examine relationships in *Prunus* focused on a limited number of cultivated species (Badenes & Parfitt 1995; Uematsu et al. 1991). In 2001 two research groups sought to clarify phylogenetic relationships among the subgenera and numerous sections of *Prunus* by examining species on a worldwide scale (Bortiri et al. 2001; Lee & Wen 2001). Unfortunately relationships among the species of section *Prunocerasus* remained unresolved. Both groups used ITS sequences and found slight variation among the native plums included in their studies. Analyses by Bortiri et al. (2001) using chloroplast *trnL-trnF* sequences also revealed only slight variation among six North American species.

Rohrer et al. (2004) used microsatellite analysis in an attempt to find molecular markers more variable among species of *Prunocerasus* than ITS or *trn* sequences. However, all pairs of species in the study shared fewer than half of their alleles, indicating greater genetic divergence among the North American plums than expected given their similar ITS and *trn* sequences. Accessions of two or three individuals of the same species often did not cluster together, suggesting that microsatellites might be too variable to be informative in resolving species relationships in *Prunocerasus*. Seeking to test the hypothesis of monophyly for *Prunocerasus* and to resolve relationships among the species, Shaw and Small (2004, 2005) turned to seven noncoding regions in the chloroplast genome shown to be highly variable across a wide array of taxa (Shaw et al. 2005). Given their taxonomically broad sampling of species both within the section and across all of *Prunus*, Shaw and Small (2004, 2005) provided unequivocal support for the monophyly of sect. *Prunocerasus*. Within the section the analyzed sequences varied little among the species. They demonstrated strong support for *P. subcordata* as sister to the rest of *Prunocerasus*. An unexpected result was the inclusion of the hairy-fruited *P. texana* within *Prunocerasus* positioned between *P. subcordata* and the other species, which formed three primary clades with little resolution within each clade. Many of the species have exemplars on more than one clade, and the chloroplast haplotypes show greater correlation with geography than species limits.

Bortiri et al. (2002) demonstrated that the nuclear gene *s6pdh* was more variable among *Prunus* species than either ITS or *trn* and showed greater promise for resolving relationships in the genus. However, only three species of *Prunocerasus* were included in their analysis. In addition, Oh and Potter (2003) reported sequences from the second intron of the nuclear gene *LEAFY* were more phylogenetically informative than either ITS or cpDNA in the rosaceous genera *Neillia* and *Stephanandra*. In this study we explore the use of these low-copy nuclear genes for resolving relationships among the species of *Prunocerasus*. Specifically we expand the use of *s6pdh* to all commonly recognized species in the section and include sequences from the second intron of *LEAFY*.

MATERIALS AND METHODS

Plant Material.—We were able to obtain at least one accession from each of the 15 (or so) species of North American plums. The exact number of species is subject to the differences in opinion concerning species circumscriptions that animate taxonomic debate. Apricot (*P. armeniaca*), cherry plum (*P. cerasifera*), and two varieties of sand cherry (*P. pumila* var. *pumila* and *P. pumila* var. *susquehanae*) were used for outgroup comparison. In all, we analyzed 37 accessions of North American plums plus the four outgroup taxa (Table 1). Some specimens were collected from wild plant populations; others were collected from cultivated plants of the University of California, Davis campus, the USDA National Clonal Germplasm Repository in Davis, and the USDA Southeastern Fruit and Nut Research Station in Byron, GA. All sources of DNA are documented by voucher specimens deposited in the University of Wisconsin-Eau Claire herbarium (UWEC). We verified identifications against published descriptions and authentic herbarium material.

DNA Extraction, Amplification, and Sequencing.—Total DNA was isolated by grinding approximately 100 mg (wet weight) of fresh or frozen leaves in liquid nitrogen and using the DNeasy Plant Mini Kit (Qiagen) according to the standard protocol. We prepared PCR reactions in 50-µl volumes containing ~10 ng

Table 1. Plant material used in study (Haplotype letters correspond to those of Shaw and Small (2005) as determined from *trnL-trnF* spacer sequences. Vouchers are collections of JRR deposited in UWEC. Key to source: state only = collected from wild; DPRU = USDA National Clonal Germplasm Repository in Davis, CA; SFNRS = USDA Southeastern Fruit and Nut Research Station in Byron, GA. Superscripted numerals preceding GenBank numbers indicate individual clones, superscripted S and L indicate direct sequenced short (750bp) and long (1000 bp) fragments).

Haplotype	Species	Voucher	Source	GenBank Accession Numbers	
	Native American Taxa			*LEAFY*	*s6pdh*
C	*P. alleghaniensis* Marshall	10,467	Michigan	EU050711	EU056679
C	*P. alleghaniensis* Marshall	10,468	Michigan	EU050712	EU056680
C	*P. americana* Marshall (glabrous)	10,495	Wisconsin	^{2}EU047724, ^{4}EU047725	^{2}EU056681, ^{3}EU056682
A	*P. americana* Marshall (glabrous)	10,505	Wisconsin	EU050713	^{2}EU056683, ^{23}EU056684
C	*P. americana* Marshall (glabrous)	10,508	Wisconsin	EU050714	^{3}EU056685, ^{4}EU056686
C	*P. americana* Marshall (hairy)	10,587	CA: DPRU 0544	^{2}EU047726, ^{3}EU447296	EU056687
C	*P. americana* Marshall (hairy)	10,607	Wisconsin	EU050715	^{2}EU056688, ^{3}EU056689
C	*P. americana* Marshall (glabrous)	10,684	Pennsylvania	EU050716	^{1}EU056690, ^{2}EU056691
C	*P. angustifolia* Marshall	10,519	Texas	EU050717	EU056692
C	*P. angustifolia* Marshall	10,588	CA: DPRU 1924	^{1}EU047727, ^{2}EU447297	EU056693
B	*P. geniculata* R. M. Harper	10,609	Florida	EU050722	EU056698
C	*P. gracilis* Engelm. & A. Gray	10,516	Texas	EU050723	EU056699
C	*P. hortulana* L. H. Bailey	10,598	CA: UCD campus	^{1}EU047728, ^{4}EU047729	EU056700
A	*P. hortulana* L. H. Bailey	10,628	GA: SFNRS	EU050724	EU056701
B	*P. maritima* Marshall	10,590	CA: DPRU 1737	EU050725	EU056702
A	*P. mexicana* S. Watson	10,511	Texas	EU050726	EU056703
A	*P. mexicana* S. Watson	10,517	Texas	EU050718	EU056694
A	*P. mexicana* S. Watson	10,518	Texas	EU050719	EU056695
A	*P. mexicana* S. Watson	10,521	Texas	EU050727	EU056704
A	*P. mexicana* S. Watson	10,545	CA: UCD campus	EU050728	EU056705
A	*P. mexicana* S. Watson	10,591	CA: DPRU 1368.1	EU050729	EU056706
C	*P. munsoniana* W. Wight & Hedrick	10,513	Texas	^{S}EU050730, ^{2}EU047730	^{1}EU056707, ^{2}EU056708, ^{3}EU056709
C	*P. munsoniana* W. Wight & Hedrick	10,592	CA: DPRU 0546	^{1}EU047731, ^{4}EU047732	^{21}EU056710, ^{23}EU056711, ^{24}EU056712
C	*P. munsoniana* W. Wight & Hedrick	10,626	GA: SFNRS	^{1}EU447298, ^{S}EU047733	EU056713
C	*P. munsoniana* W. Wight & Hedrick	10,676	Pennsylvania	^{1}EU047744, ^{3}EU047745	
A	*P. murrayana* E. J. Palmer	10,524	Texas	EU050731	EU056715
A	*P. murrayana* E. J. Palmer	10,525	Texas	^{L}EU050732, ^{S}EU050733	EU056716
A	*P. murrayana* E. J. Palmer	10,526	Texas	EU050734	EU056717
A	*P. nigra* Aiton	10,606	Wisconsin	EU050735	EU056718

Table 1. continued.

Haplotype	Species	Voucher	Source	GenBank Accession Numbers	
	Native American Taxa			***LEAFY***	***s6pdh***
A	*P. nigra* Aiton	10,633	Wisconsin	EU050736	EU056719
C	*P. rivularis* Scheele	10,514	Texas	[5]EU447299, [1]EU047739, [2]EU047740, [21]EU047734, [24]EU047735	[1]EU056721, [22]EU056722
C	*P. rivularis* Scheele	10,527	Texas	[2]EU047741, [3]EU047736, [22]EU047742, [24]EU447300, [25]EU447301	[2]EU056723, [3]EU056724
C	*P. rivularis* Scheele	10,528	Texas	[1]EU047743, [2]EU047737, [3]EU047738	[2]EU056725, [4]EU056726
S	*P. subcordata* Benth.	10,595	CA: DPRU 2296	EU050739	EU056727
T	*P. texana* D. Dietr.	10,685	Texas	EU050741	EU056729
C	*P. umbellata* Elliott	10,520	Texas	EU050742	[3]EU056730, [4]EU056731
C	*P. umbellata* Elliott	10,620	GA: SFNRS	EU050743	EU056732
	Outgroups				
	P. armeniaca L.	10,589	CA: DPRU 1134	EU050720	EU056696
	P. cerasifera Ehrh.	10,541	California	EU050721	EU056697
	P. pumila L. var. *pumila*	10,611	Wisconsin	EU050737	EU056720
	P. pumila var. *susquehanae* (Willd.) H. Jaeger	10,445	Wisconsin	EU050740	EU056728

of genomic DNA, 1.25 units of *ExTaq* DNA polymerase (Takara), 1x PCR buffer, 200 µM dNTPs, 0.2 µM of each primer, and sterile water. Intron 2 of the nuclear gene *LEAFY* was amplified using primers modified from Oh and Potter (2003): LFY5: 5'-CAGAACATTGCCAAGGAGC-3', LFY4: 5'-GGCTTGTTGATGTAGCT-TGC-3'; and nuclear gene *s6pdh* from Exon 2 to Exon 6 was amplified using primers modified from Bortiri et al. (2002) plus a new primer (o): *s6pdh*-k: 5'-CAAGAGTGAAGCAGACGTTGG-3', *s6pdh*-h: 5'-AGACCA-ATGCTACGAACTAGGCCG-3', *s6pdh*-o: 5'-AGAATAAGGTGTTGGACATAGACG-3', *s6pdh*-p: 5'-AGAGTG-GTCCTGGATTTCTTATCTA-3'. Thirty-five cycles of three-step PCR, preceded by an initial melting step of 4 min at 94°C and concluded by a final extension of 7 min at 72°C, were carried out as follows: denaturation at 94°C for 30 sec, primer annealing at 52°C (*LEAFY*) or 54°C (*s6pdh*) for 1 min, and extension at 72°C for 2 min.

Following electrophoresis we excised PCR products from 1% agarose gels and purified them using a QIAquick Gel Extraction Kit (Qiagen). We sent the fragments for direct sequencing using the PCR primers either to Davis Sequencing (Davis, CA) or the DNA Sequence Laboratory of the University of Wisconsin Biotechnology Center (Madison, WI). PCR products with unreadable sequences or a significant number of ambiguous base calls were cloned using the TOPO TA Cloning Kit for Sequencing (Invitrogen) following the manufacturer's instructions. Sequencing of all clones using T3 and T7 primers was done by the DNA Sequence Laboratory of the UW Biotechnology Center. Following cloning, sequences with possible PCR artifacts were identified and removed from further analysis by comparing the cloned sequences to each other and to the original chromatogram obtained through direct sequencing. When two or more clones yielded identical sequences, only one was used in the analyses.

Each sequence chromatogram was scrutinized for base determination errors using Chromas 2.22 (Technelysium Pty Ltd), and the sequences were aligned by eye in GeneDoc 2.6.002 (Nicholas & Nicholas 1997). The close relationship among *Prunus* species made manual alignment of the sequences straightforward. For data analysis, parsimony informative indels were coded as additional binary characters. Seven indels were included for *LEAFY* and eight for *s6pdh*. *LEAFY* sequences were trimmed to just Intron 2; *s6pdh* sequences were truncated to begin 18 bp downstream from the end of primer k, located in Exon 2, and end 14 bp upstream from the start of primer p in Exon 6. Sequences were submitted to GenBank (accession numbers listed in Table 1).

Phylogenetic Analyses.—Both data sets were analyzed using maximum parsimony (MP) with PAUP* 4.0b10 (Swofford 2002) and Bayesian inference (BI) with MrBayes 3.1.2 (Huelsenbeck & Ronquist 2001; Ronquist & Huelsebeck 2003). Two heuristic MP searches with TBR branch swapping and the Multrees option were performed: the first with MaxTrees set to one million; in the second, the "nchuck" and "chuckscore" options were employed so that 10,000 trees were saved and swapped for each of 30 random addition replicates. The results of each search were summarized as strict consensus cladograms. Relative support for each branch was assessed by heuristic searches of 1000 bootstrap replications with 10 random addition replicates each and TBR branch swapping. For each random addition replicate 100 trees were saved. For BI analyses each data set was partitioned into nucleotide characters and indel characters. ModelTest 3.7 (Posada & Crandall 1998) was used to select the substitution model that best fit the nucleotide data using the Akaike information criterion: TVMef for *LEAFY* and HKY+I+G for *s6pdh*. Each of two BI runs for each gene consisted of three heated and one cold chain with samples drawn every 100 generations. We ran the *LEAFY* data for 1,000,000 generations discarding the first 500,000 generations, whereas for *s6pdh* we ran 1,500,000 generations discarding the first 750,000 generations. The runs for each data set were combined and a majority rule consensus tree constructed with a 67% threshold.

Determination of chloroplast haplotypes.—In order to compare our phylogenetic results from nuclear *LEAFY* and *s6pdh* with those of Shaw and Small (2004, 2005), we sequenced the *trnL-trnF* intergenic spacer from the chloroplast genome for our accessions. We amplified the spacer using the e-f primer pair of Taberlet et al. (1991) and used primer e, and sometimes primer f, for sequencing (GenBank accessions EU606152–EU606192). We aligned our sequences with those from the 18 *Prunocerasus* exemplars used in Shaw and Small

(2004). The maximum parsimony tree from the combined dataset was used to place each of our native plum accessions into one of the primary chloroplast haplotypes (A, B, C, S, or T) of Shaw and Small (2005).

RESULTS

For clarity in the results and discussion sections we refer to specific sequences by their names on the phylograms, omitting the genus name and differentiating among clones from the same collection by decimels following the last three digits of the collection number.

LEAFY Alignment and Data Analysis.—PCR with primers LFY5 and LFY4 yielded fragments approximately 750 or 1000 nucleotides in length, the difference being a 250-bp insertion. Only 1000-bp fragments were PCR amplified for *Prunus hortulana* and *P. murrayana*. All three individuals of *P. rivularis* and two of the four collections of *P. munsoniana* (513, 676) had both 750 and 1000-bp fragments (Fig 1). The other collections of *P. munsoniana* and the remainder of the species yielded only 750-bp fragments. Some of the cloned *P. rivularis* sequences appeared to be recombinations of the 750 and 1000-bp sequences, similar to those of *P. angustifolia* and *P. hortulana*/*P. murrayana* respectively (Fig 2). Putative recombinant sequences were omitted from the phylogenetic analyses. Trimmed to *LEAFY* Intron 2, the ingroup sequences varied in length from 658 bp in *P. texana* to 925 bp in one clone of *P. rivularis* (528.22). The final alignment used in the *LEAFY* data analysis included 930 nucleotide characters, of which 856 were invariant, 35 varied but were parsimony-uninformative, and 39 (4.2%) were parsimony informative for the ingroup taxa.

The strict consensus MP cladograms from the two parsimony analyses are identical (not shown), each of length 194 with consistency index (CI) of 0.634 and retention index (RI) of 0.796. Their topologies are similar to the Bayesian analysis phylogram (Fig. 3), but several nodes (indicated by the solid circles) are collapsed and there are minor rearrangements within Clades 3 and 4 (topology indicated by dotted lines). Species of *Prunus* sect. *Prunocerasus* form a monophyletic group split into three lineages: *P. subcordata* plus Clades 1 and 2. Clade 3 is composed of *P. angustifolia* and *angustifolia*-like sequences from *P. munsoniana* and *P. rivularis*. The latter two species (names in bold on Fig. 3) also have cloned sequences from the same individuals on Clade 2. Relationships among *P. americana*, *P. mexicana*, and *P. nigra* are unresolved; they diverge from a basal polytomy on Clade 2. Sequences of Clade 4, including those of *P. hortulana*, *P. murrayana* (except 525S), *P. munsoniana*, and *P. rivularis*, have a 250-bp insertion not found among the other sequences.

s6pdh Alignment and Data Analysis.—The final alignment for the *s6pdh* analysis includes 1272 nucleotide characters, of which 1197 were invariant, 46 varied but were parsimony-uninformative, and 29 (2.3%) were parsimony informative for the *Prunus* sect. *Prunocerasus* species. The shortest sequences among the ingroup were those of *P. hortulana* (628), *P. maritima*, and *P. subcordata* at 1204 nucleotides, including 7 or 8 TC repeats in Intron 3, whereas one *P. americana* clone (505.2) had the longest sequence at 1256 nucleotides with 31 TC repeats.

Just as in the *LEAFY* analyses, the strict consensus MP cladograms from both parsimony analyses of *s6pdh* are identical (not shown) and have lengths of 153, consistency indices (CI) of 0.699, and retention indices (RI) of 0.854. The MP cladograms are nearly identical to the BI phylogram (Fig. 4). On the MP cladograms, Clades 5 and 6 are sister groups such that *Prunus* sect. *Prunocerasus* forms a monophyletic group, albeit with bootstrap support less than 50%, the branch indicated by the black circle is collapsed, and *americana*.684.1 is sister to *americana*.495.3/*americana*.505.23 on Clade 5 (indicated by dotted lines). Clade 5 includes *P. subcordata* plus *subcordata*-like sequences from five individuals of *P. americana* and one of *P. munsoniana*. These accessions (names in bold on Fig. 4) also have sequences on Clade 6, which includes all the other native plum taxa. There is poor resolution among these taxa. *Prunus angustifolia*, *P. texana*, and *angustifolia*-like sequences from *P. munsoniana* and *P. rivularis* compose Clade 7. Clade 8 consists solely of *P. americana* and *P. mexicana*, plus a similar sequence from one individual of *P. umbellata* (520.4), which also has a sequence among the taxa of the Clade 6 basal polytomy (*umbellata*.520.3).

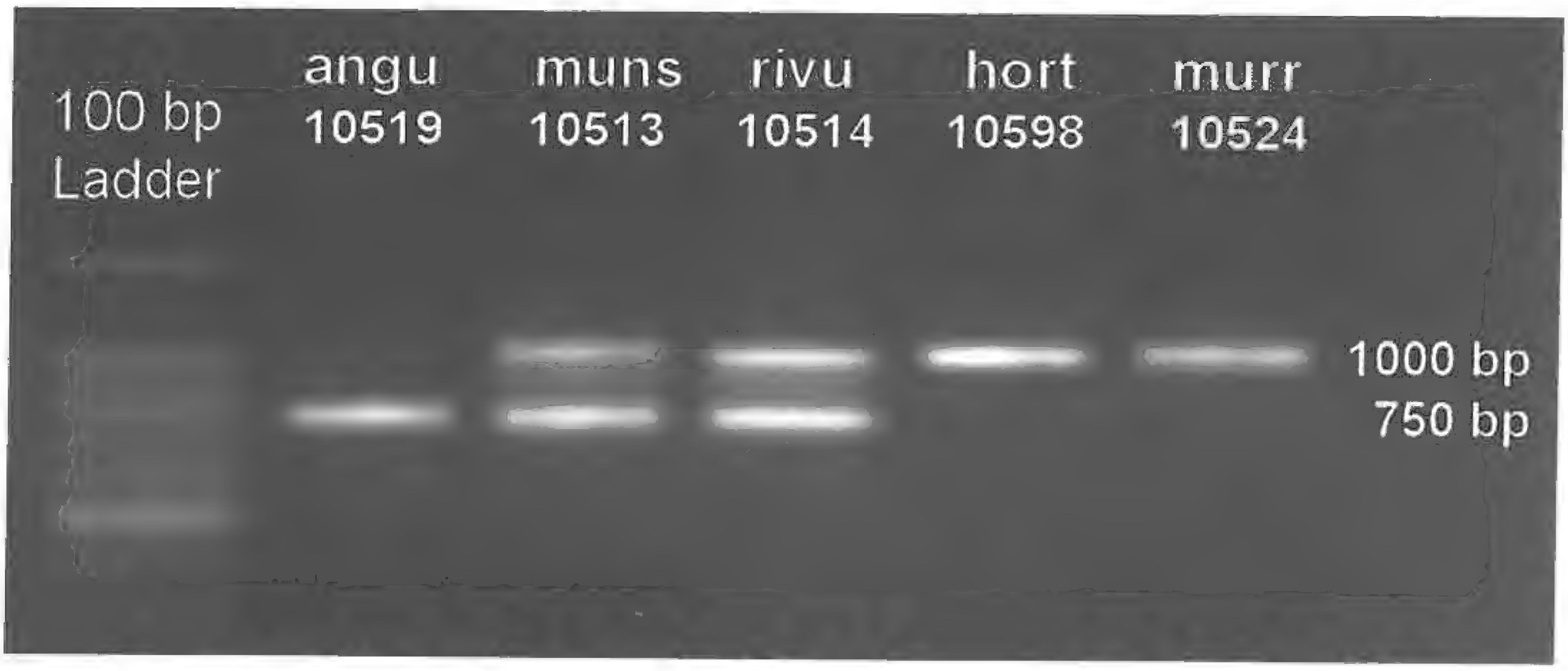

Fig. 1. Gel following electrophoresis of PCR products using LFY 5 and LFY 4 primers.

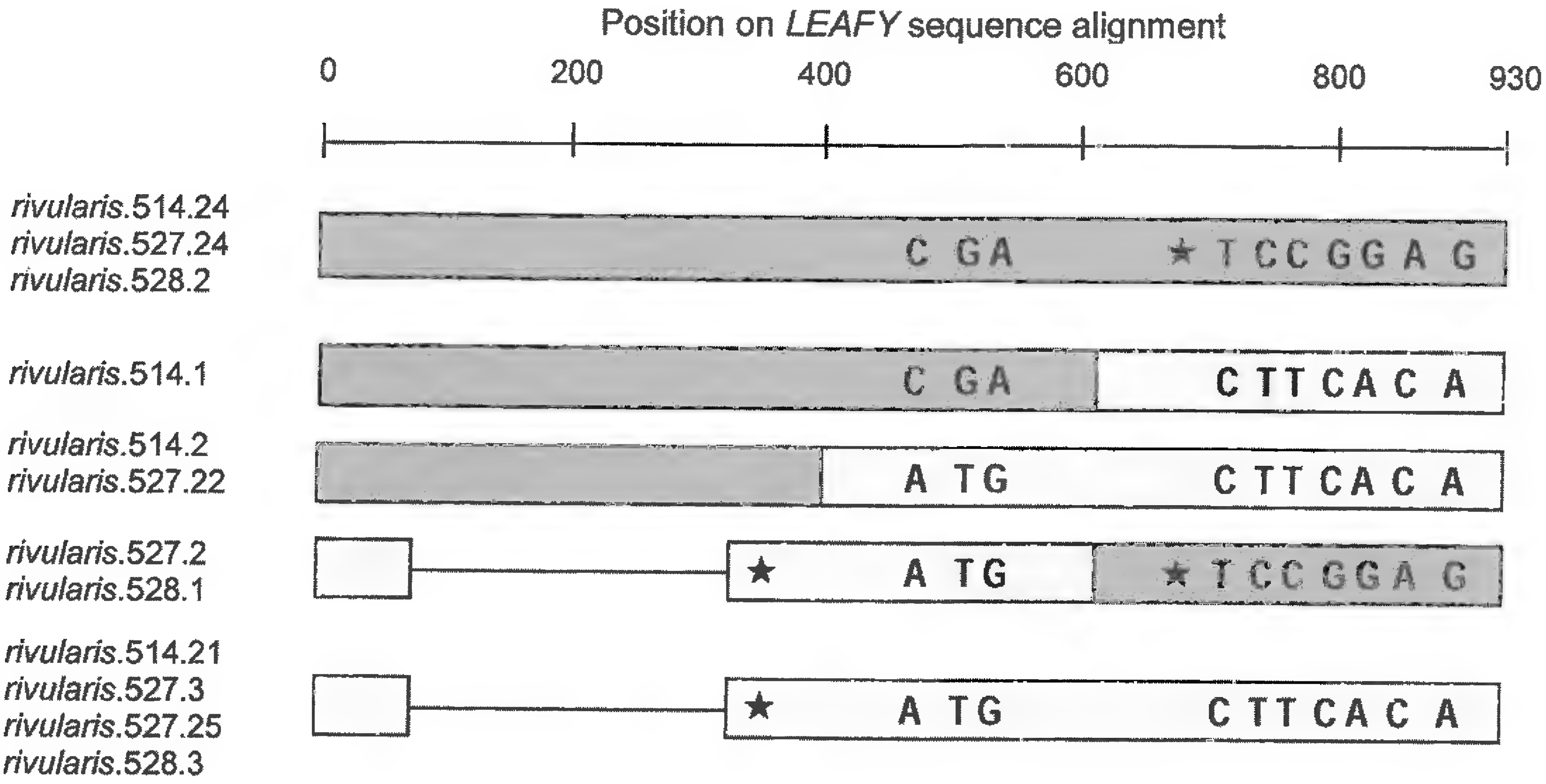

Fig. 2. Graphic representation of cloned *LEAFY* sequences from *Prunus rivularis* accessions. Each bar represents DNA sequence. Dark gray segments correspond to close relationship with *P. hortulana* and *P. murrayana* sequences (Clade 4 on Fig.3) and light gray segments correspond to close relationship with *P. angustifolia* sequences (Clade 3 on Fig. 3). Characters used to map sequence segments: straight line indicates absence of 250-bp insertion (alignment gap), stars indicate the presence of 6-bp and 9-bp deletions, and letters indicate key nucleotide differences between the *hortulana*-type and *angustifolia*-type sequences. The boundaries between sequence types are drawn to within about 75 bp.

DISCUSSION

The nuclear genes *LEAFY* and *s6pdh* provide weak resolution of relationships among species of *Prunus* sect. *Prunocerasus*. The majority of taxa diverge from polytomies on the MP consensus and BI trees. The topology of these trees is different from the cpDNA cladogram of Shaw and Small (2005) where *P. subcordata* and then *P. texana* are sister groups to the remaining species, which segregate into three primary clades: American

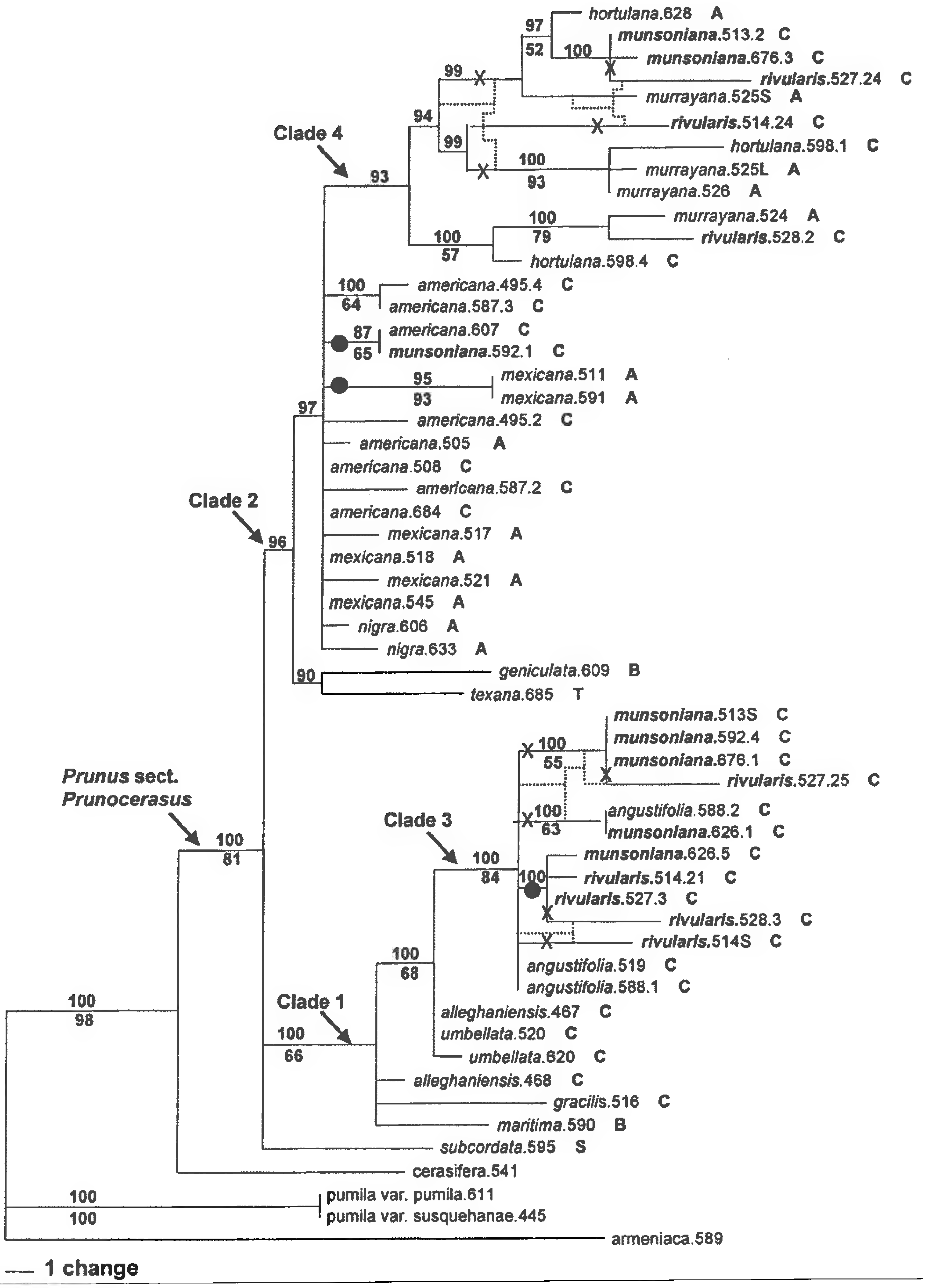

FIG. 3. *LEAFY* 67% majority rule consensus phylogram from Bayesian analysis. Ingroup taxa are italicized; outgroup taxa are in roman type. Support values above the branches are the BI posterior probabilities (%) for each clade; below branches are MP bootstrap values over 50%. MP strict consensus cladograms differ where black circles indicate branches that collapse, and branches cut at X's are reconnected as shown by dotted lines. Taxa are labeled by epithet plus last 3 digits of collection number (and clone number). Letters following the taxon names correspond to cpDNA haplotypes of Shaw and Small (2005) as determined from *trnL-trnF* spacer sequences.

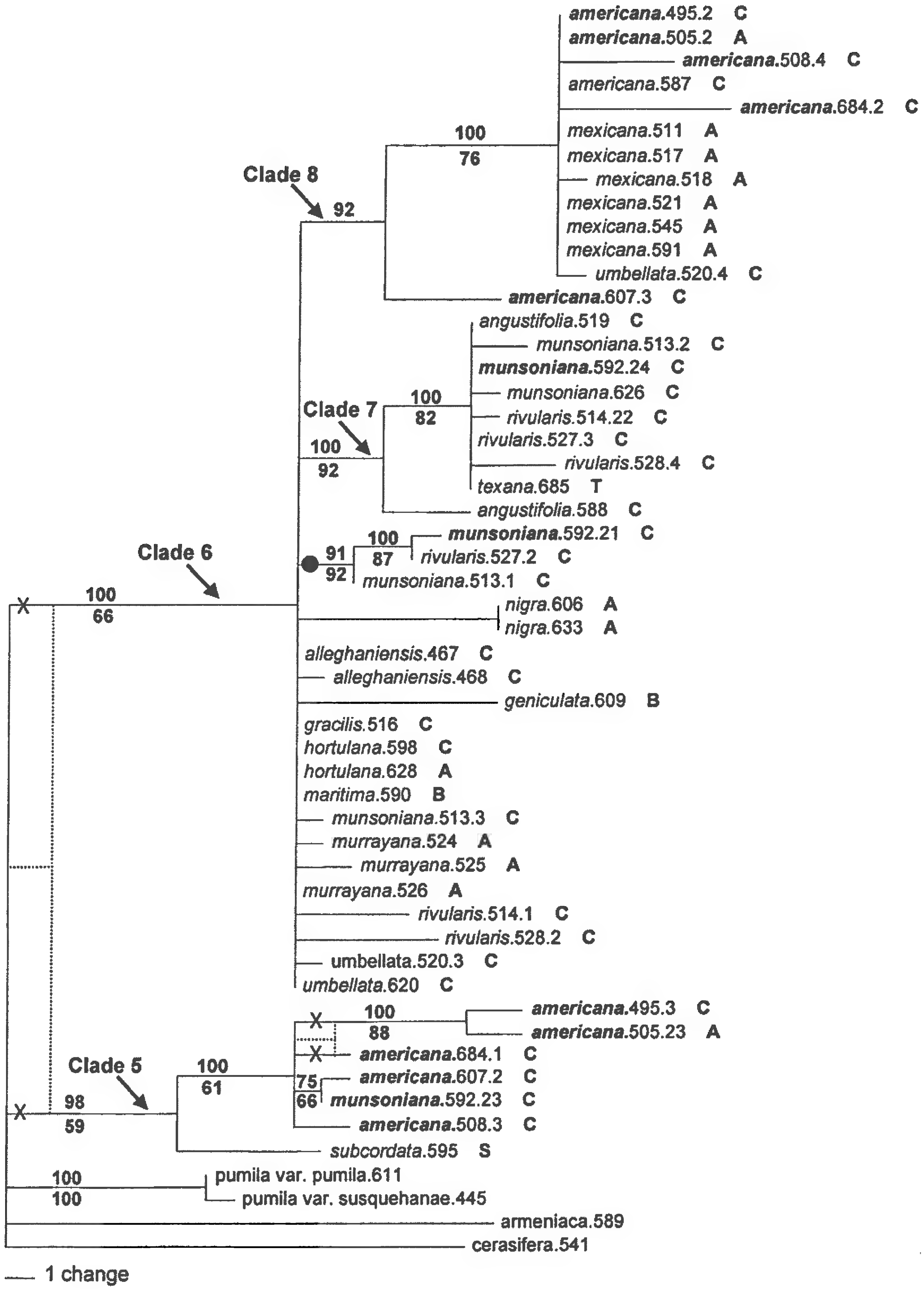

Fig. 4. *s6pdh* 67% majority rule consensus phylogram from Bayesian analysis. Ingroup taxa are italicized; outgroup taxa are in roman type. Support values above the branches are the BI posterior probabilities (%) for each clade; below branches are MP bootstrap values over 50%. MP strict consensus cladograms differ where black circle indicates branch that collapses, and branches cut at X's are reconnected as shown by dotted lines. Taxa are labeled by epithet plus last 3 digits of collection number (and clone number). Letters following the taxon names correspond to cpDNA haplotypes of Shaw and Small (2005) as determined from *trnL-trnF* spacer sequences.

(A), Beach (B), and Chickasaw (C). Clade 1 on the *LEAFY* tree and *s6pdh* Clades 5 and 7 consist largely of accessions with cpDNA haplotype C, otherwise taxa on the nuclear gene trees do not resolve into the A, B, and C clades of Shaw and Small (2005). Incongruence between chloroplast and nuclear phylogenies is common and typically attributed to such factors as hybridization, lineage sorting, or long-branch attraction (Albaladejo et al. 2005; Doyle 1997; Maddison 1997; Sang & Zhong 2000). The geographic distribution of the chloroplast ABC clades suggests introgression with chloroplast capture given the ease with which North American plums are known to hybridize (Hedrick 1911; Shaw & Small 2004).

Although *Prunus texana*, known as peachbush or Texas wild peach, has historically been placed in sect. *Amygdalus* due to its hairy-skinned fruit, Shaw and Small (2004) found that it has a plum chloroplast genome. Evidence from the nuclear genes *LEAFY* and *s6pdh* confirms its placement in sect. *Prunocerasus*. On the cpDNA cladogram *P. texana* was sister to the other plums of eastern North America, a position we could not confirm. It is sister to *P. geniculata*, the rare endemic of the Lake Wales Ridge in central Florida, on our *LEAFY* phylogram. However, this relationship is based on one character change and has weak bootstrap support. On the *s6pdh* phylogram *P. texana* is part of Clade 7 with *P. angustifolia* and the *angustifolia*-like sequences of *P. munsoniana* and *P. rivularis*.

Prunus alleghaniensis, P. gracilis, P. maritima, and *P. umbellata* form a paraphyletic group on *LEAFY* Clade 1, basal to Clade 3. These four species clustered on the UPGMA dendrogram based on similarity of microsatellite markers in the study of Rohrer et al. (2004). These species closely resemble each other morphologically and were allied by early students of American plums such as Wight (1915). On the *s6pdh* cladogram, they are part of the large Clade 6 basal polytomy.

Prunus americana and *P. mexicana* can be difficult to separate morphologically, especially when working with herbarium specimens. Similarly their *LEAFY* and *s6pdh* sequences were similar and without resolution into monophyletic *P. americana* and *P. mexicana* groups. On the *LEAFY* phylogram the *P. americana* and *P. mexicana* sequences diverge from a basal polytomy along with *P. nigra*, *munsoniana*.592.1, and Clade 4. *LEAFY* sequences *americana*.508 (WI), *americana*.684 (PA), *mexicana*.518 (TX), and *mexicana*.545 (cult.) differ trivially by the length of a poly-A run and some nucleotide characters heterozygous for one or two sequences but with only one of the two bases on the other sequences. Otherwise they are identical.

Although our data do not separate *Prunus americana* from *P. mexicana* sequences on either *LEAFY* Clade 2 or *s6pdh* Clade 8, Boonprakob et al. (2001) calculated a UPGMA dendrogram, based on similarities of RAPD markers, on which all 13 of their accessions of *P. americana* clustered together and distinct from a cluster of all 11 accessions of *P. mexicana*. Clearly more collections with a wide geographic distribution and more genes will need to be examined and correlated with the morphological characteristics of those accessions before the taxonomic structure of the *P. americana-mexicana* complex is understood.

In an earlier microsatellite study, Rohrer et al. (2004) included two collections from east Texas near Marshall (designated *P.* sp. (*americana* x *mexicana*?) 10517 and 10518 in that publication) that are morphologically intermediate between typical *Prunus americana* and *P. mexicana*. The lack of differentiation between *P. americana* and *P. mexicana LEAFY* and *s6pdh* sequences leaves their determination ambiguous. However, because neither 517 nor 518 have a *subcordata*-like *s6pdh* sequence and because most modern floras exclude *P. americana* from Texas, we have provisionally determined these accessions to be *P. mexicana*.

Two distinct sequences were isolated from five of the six accessions of *Prunus americana* by cloning their *s6pdh* PCR products. One sequence from each pair is on Clade 8 along with *P. mexicana* and the single sequence of *P. americana* 587; the other is on Clade 5 with *P. subcordata*. Given that these *P. americana* sequences form a monophyletic group sister to *P. subcordata* and that *P. subcordata* grows only in California and Oregon, far west of *P. americana* range in eastern North America, it seems unlikely that the five *P. americana* collections with two *s6pdh* sequences are recent hybrids independently involving *P. subcordata*. If *s6pdh* is a single copy gene in all diploid *Prunus* species as concluded by Bortiri et al. (2002) and if *P. americana* is diploid as it is reported to be ($2n$ = 16, Löve & Löve 1982), then a high degree of heterozygosity is being maintained at a single locus. However, we cannot rule out the possibility that there are two heterologous

ancestral *s6pdh* loci across *Prunus* with only one or the other copy observed in most North American plums, or alternatively gene duplication in *P. americana*. Bortiri et al. (2002) found divergent *s6pdh* sequences in *Prunus caroliniana* and *P. emarginata*. They hypothesized that divergent paralogs in *P. caroliniana*, a tetraploid species, may have arisen through gene duplication associated with polyploidization. In *P. caroliniana* the inferred polypeptides of the divergent clones differed at 16 of 251 amino acids (Bortiri et al. 2002), whereas for each of our five accessions of *Prunus americana* with divergent *s6pdh* sequences, the inferred polypeptides of the two clones differ by only 1–4 out of 223 amino acids. To better explain the existence of divergent sequences in *P. americana*, it would be useful to have chromosome counts from each of those accessions to verify that they are indeed diploid. Also because Southern blotting with a *Malus domestica* cDNA *s6pdh* probe by Bortiri et al. (2002) detected more than one region of sequence similarity in several genera of Rosaceae, the possibility of paralogous genes might be further investigated.

Alleles closely related to those of *Prunus americana*, and possibly *P. mexicana*, were found in other plum species suggesting introgression. *Prunus munsoniana* 592 has both *s6pdh* and *LEAFY* sequences monophyletic with sequences from *P. americana* 607. On the *s6pdh* tree *munsoniana* 592.23 is nested with the five *subcordata*-like *P. americana* clones and has the same amino acid sequence as *americana*.495.3 and *americana*.505.23. On the *LEAFY* tree *munsoniana*.592.1 is sister to *americana*.607. Also *P. umbellata* 520 has an *americana/mexicana*-type *s6pdh* sequence (*umbellata*.520.4) in addition to a sequence similar to that of the *P. umbellata* 620 collection.

Sequences from both *LEAFY* and *s6pdh* suggest that *Prunus rivularis* may be an allopolyploid with *P. angustifolia* as one parent. The *LEAFY* sequences further suggest that the other parent is most likely *P. hortulana* or *P. murrayana* and that recombination between parental sequences has taken place. Three or four distinct sequences were cloned from each of the *P. rivularis* accessions. *LEAFY* is believed to be a single-copy nuclear gene (Frohlich & Parker 2000; Oh & Potter 2003) and would be expected to have one or two alleles in a diploid species. At least one sequence from each *P. rivularis* accession is monophyletic with sequences of *P. angustifolia* (Clade 3 on the *LEAFY* phylogram and Clade 7 on the *s6pdh* phylogram). The other sequence is on Clade 4 of *LEAFY* along with sequences of *P. hortulana* and *P. murrayana*. In addition, some *LEAFY* recombinant sequences were cloned where part of the sequence matches *P. angustifolia* and the rest matches *P. hortulana/murrayana* (graphically illustrated on Fig. 2). Although it is possible for recombinant sequences to arise as PCR artifacts (Cronn et al. 2002; Posada et al. 2002), in our study they were isolated only from *P. rivularis* and they were found among the *LEAFY* sequences of all three *P. rivularis* accessions. This would seem to support the hypothesis that the recombinant sequences arose through meiotic recombination following hybridization between *P. angustifolia* and either *P. hortulana* or *P. murrayana*. Given the few phylogenetically-informative characters in the *s6pdh* data, if there were recombinant *s6pdh* sequences, we were unable to identify them.

Plants in our study determined as *Prunus munsoniana* appear to be a mixture of hybrids having *P. angustifolia* as one of the parents. All four *P. munsoniana* collections have a *LEAFY* sequence on Clade 3 with *P. angustifolia* and *P. rivularis*, and three collections have *s6pdh* sequences on Clade 7, again with *P. angustifolia* and *P. rivularis* (we are lacking a *s6pdh* sequence for *P. munsoniana* 676). Two *P. munsoniana* collections (513 and 676) have a second *LEAFY* sequence with the 250-bp insertion found also among sequences of *P. hortulana*, *P. murrayana*, and *P. rivularis* on Clade 4. On the BI cladogram, *munsoniana*.513.2 and *munsoniana*.676.3 form a trichotomy with *rivularis*.527.24, but on the MP cladogram they are sister to *hortulana*.628. Thus, these two *P. munsoniana* collections have *LEAFY* sequences closely related to those of *P. rivularis*, which lends support to the suggestion by Diggs et al. (1999) that *P. munsoniana* is simply a larger version of *P. rivularis*. However, the other two specimens of *P. munsoniana* (592 and 626) lack *hortulana/murrayana*-like *LEAFY* sequences, yet are very similar morphologically to 513 and 676. For *P. munsoniana* 626 we were only able to isolate *angustifolia*-like *LEAFY* sequences. Likewise we isolated only a single *s6pdh* sequence, which lies on Clade 7 with *P. angustifolia* and *P. rivularis*. *P. munsoniana* 513 and 592 each yielded three distinct *s6pdh* sequences, suggesting that at least some *P. munsoniana* specimens may be allopolyploids. *P. munsoniana* 592

has a sequence on *s6pdh* Clade 7 (592.24) with *P. angustifolia*, and on Clade 5 (592.23) sister to a clone of *P. americana* (607.2), just as on the *LEAFY* phylogram. The third *s6pdh* sequence (592.21) is sister to *rivularis*.527.2 and these two are sister to *munsoniana*.513.1.

To our knowledge we are the first to suggest a close phylogenetic relationship between *Prunus murrayana* and *P. hortulana* (Clade 4 on the *LEAFY* phylogram). *P. murrayana*.525L and *murrayana*.526 form a clade with *hortulana*.598.1 having 93% MP bootstrap support and 100% BI posterior probability. The *s6pdh* sequences do not confirm or refute the close relationship between *P. murrayana* and *P. hortulana*, because their sequences along with those of *P. alleghaniensis, P. geniculata, P. gracilis*, and several other species all are unresolved on the Clade 6 basal polytomy. Until a decade ago, *P. murrayana* was a poorly known species endemic to Texas west of the Pecos River and represented in herbaria by only a handful of specimens. When originally described, Palmer (1929) wrote that it might be most closely related to *P. rivularis*. Enquist (1997) formalized this relationship by designating *P. murrayana* as a synonym when he described *P. rivularis* var. *pubescens* Enquist. He discovered numerous plums on the western side of the Edwards Plateau with pubescent first-year branchlets, pubescent pedicels, and pubescence encircling the petioles, and he concluded that these plants were the same taxon as *P. murrayana* known from further west. Many of Enquist's collections are morphologically well matched with authentic *P. murrayana* specimens. He explained how most of the apparent differences between *P. murrayana* and *P. rivularis* did not hold in light of the new collections and that the only distinguishing character was pubescence; the branchlets, pedicels, and petioles of *P. rivularis* are glabrous or nearly so (Enquist 1997). Clade 4 of the *LEAFY* phylogram includes not only *P. hortulana* and *P. murrayana* but also sequences from all three accessions of *P. rivularis* and a couple from *P. munsoniana*. Our *P. murrayana* collections are from Coke and Tom Greene Counties east of the Pecos River at localities where Enquist (1997) collected *P. rivularis* var. *pubescens* [= *P. murrayana*]. These collections have only Clade 4 *LEAFY* sequences, whereas our three collections of *P. rivularis* have both Clade 4 and Clade 3 sequences. Similarly, *P. murrayana* accessions have *s6pdh* sequences only from the Clade 6 polytomy, whereas all three *P. rivularis* accessions have a cloned sequence on Clade 7 with *P. angustifolia* and from the basal polytomy of Clade 6. We believe that *P. murrayana* is a diploid species distinct from *P. rivularis*, which we believe is an allopolyploid derived from *P. angustifolia* and either *P. murrayana* or *P. hortulana*.

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RECOGNITION OF THREE TAXA OF EASTERN NORTH AMERICAN "*WALDSTEINIA*" AND THEIR APPROPRIATE NAMES WHEN INCORPORATED INTO *GEUM* (COLURIEAE: ROSACEAE)

Alan S. Weakley

University of North Carolina Herbarium (NCU)
North Carolina Botanical Garden, UNC-Chapel Hill
Campus Box 3280
Chapel Hill, North Carolina 27599-3280, U.S.A.
weakley@unc.edu

Kanchi N. Gandhi

Harvard University Herbaria (GH)
22 Divinity Avenue
Cambridge, Massachusetts 02138-2094, U.S.A.
gandhi@oeb.harvard.edu

ABSTRACT

We review the nomenclatural and taxonomic history of eastern North American species traditionally treated in the genus *Waldsteinia* Willd. (Rosaceae), and conclude that it is desirable to recognize three taxa (as has been done with rare exceptions) and to place these in the genus *Geum* L. Given the equivocal morphological data and absence of molecular data on which to assess the relationship of the three taxa, the most conservative treatment is to place them at the same (species) rank. A new combination is made in *Geum* for the southeastern United States taxon variously treated as *W. parviflora* Small, *W. fragarioides* (Michx.) Tratt. var. *parviflora* (Small) Fernald, *W. doniana* Tratt., or *W. fragarioides* ssp. *doniana* (Tratt.) Teppner (the latter not effectively published): **Geum donianum** (Tratt.) Weakley & Gandhi, comb. nov.

RESUMEN

Se revisa la historia taxonómica y nomenclatural de las oriental Estados Unidos especies tratadas tradicionalmente en el género *Waldsteinia* Willd. (Rosaceae), y se concluye que es deseable reconocer tres taxa (como se ha hecho con raras excepciones) y colocarlos en el género *Geum* L. Dados los datos morfológicos equívocos y la ausencia de datos moleculares en los que apoyar la relación entre los tres taxa, el tratamiento más conservador es colocarlos en el mismo rango (especie). Se hace una nueva combinación en *Geum* para el taxon del sudeste de los Estados Unidos tratado variablemente como *W. parviflora* Small, *W. fragarioides* (Michx.) Tratt. var. *parviflora* (Small) Fernald, *W. doniana* Tratt., o *W. fragarioides* ssp. *doniana* (Tratt.) Teppner (este último no publicado efectivamente): ***Geum donianum*** (Tratt.) Weakley & Gandhi, comb. nov.

Recent investigations in the taxonomy of tribe Colurieae Rydberg of the Rosaceae have led to the conclusion that *Waldsteinia* Tratt. is phylogenetically embedded within *Geum* L. and should be combined with it (Smedmark 2006). Smedmark (2006), Smedmark et al. (2003), and Smedmark and Eriksson (2002) presented strong evidence that *Waldsteinia* is involved in ancient allopolyploidization from which parts of *Geum* have arisen, and they argue that the most reasonable circumscription of the genus is to include all the perennial herbs of Geinae involved in the reticulate evolution. Morphologically, *Waldsteinia* is comfortably congruent within a broadly defined *Geum*, differing only in the style dehiscent at its base; and *Geum* (in a narrower sense) already includes a wide diversity of style morphologies, apparently adaptations to a variety of pollination and dispersal mechanisms.

Most North American workers have accepted three taxa of *Waldsteinia* for eastern North America: Taxon A ("*fragarioides*," sensu stricto), a northern larger-petaled entity with trifoliolate leaves; Taxon B ("*parviflora*" or "*doniana*"), a southern smaller-petaled entity with trifoliolate leaves; and Taxon C ("*lobata*"), a Southern Appalachian endemic with small petals and lobed, rather than trifoliolate, leaves (Table 1). A notable exception to the acceptance of Taxon A and Taxon B as distinct at some formal taxonomic level is the treatment of Radford et al. (1968), which lumps Taxa A and B and does not mention *W. lobata*, reported for the Carolinas by earlier authors. Smedmark (2006) made transfers into *Geum* of *Waldsteinia* species, but regarded Taxon B as a synonym of Taxon A (without explanation, but perhaps because of the nomenclatural and taxonomic confusion discussed below), leaving it without a name in *Geum*.

Although their acceptance as taxa has been nearly universal, the appropriate taxonomic level at which to recognize these entities (species, subspecies, or variety) has remained controversial and variable (Table 1).

Table 1. A comparison of recent taxonomic treatments of the *"Waldsteinia"* taxa of eastern North America.

Treatment	Taxon A: fragarioides	Taxon B: doniana/parviflora	Taxon C: lobata
Small (1898)	*Waldsteinia fragarioides*	*Waldsteinia parviflora*	*Waldsteinia lobata*
Rydberg (1913)	*Waldsteinia fragarioides*	*Waldsteinia doniana*	*Waldsteinia lobata*
Small (1933)	*Waldsteinia fragarioides*	*Waldsteinia doniana*	*Waldsteinia lobata*
Fernald (1950)	*Waldsteinia fragarioides* var. *fragarioides*	*Waldsteinia fragarioides* var. *parviflora*	{out of area treated}
Gleason (1952)	*Waldsteinia fragarioides*	*Waldsteinia parviflora*	{out of area treated}
Teppner (1968)	*Waldsteinia fragarioides* ssp. *fragarioides*	*Waldsteinia fragarioides* "ssp. *doniana*"	*Waldsteinia lobata*
Radford, Ahles, & Bell (1968)	**Waldsteinia fragarioides**		{not treated}
Gleason & Cronquist (1991)	*Waldsteinia fragarioides* var. *fragarioides*	*Waldsteinia fragarioides* var. *parviflora*	{out of area treated}
Kartesz 1999	*Waldsteinia fragarioides* ssp. *fragarioides*	*Waldsteinia fragarioides* "ssp. *doniana*"	*Waldsteinia lobata*
Smedmark (2006)	**Geum fragarioides**		*Geum lobatum*
Weakley & Gandhi (this paper)	*Geum fragarioides*	*Geum donianum*	*Geum lobatum*
Phipps in FNA (in prep.)	*Waldsteinia fragarioides*	*Waldsteinia doniana*	*Waldsteinia lobata*

A review of literature and specimens reveals that three taxa should be recognized in eastern North America. Habitally quite similar, the three taxa differ from one another in details of leaf lobing/division and petal size, the combination of characters strongly correlated with coherent geographic distributions. Though imperfect herbarium specimens may be difficult to interpret, there seem to be no true intermediates, nor is their clinal variation in petal size. Moreover, the "*Waldsteinia* group" of *Geum* is morphologically conservative, with relatively minor morphological characters separating taxa on different continents (such as the North American *G. fragarioides* and the Eurasian *G. ternatum* (Stephan) Smedmark. Indeed, the morphological relationships of the three taxa make the closer affinity of Taxon B problematic (if leaf lobing is the more phylogenetically revealing character, then Taxon B may be more closely related to Taxon A, but lacking molecular data it is plausible that the floral characters are more phylogenetically revealing, and taxa B and C are more closely related, forming a southern, small-petaled clade). For these reasons, we agree with Phipps (in prep.) that the best current (and conservative) taxonomic treatment of the "*Waldsteinia* group" in eastern North America is as three species.

Nomenclature has also been contentious, with disagreement as to the appropriate basionym ('doniana' or 'parviflora') to apply to Taxon B (Table 1). Fernald (1935) believed that the application of the epithet '*doniana*' to the small-petaled southern taxa was a misapplication. He argued that the type plate "seems to me a garden-development in which, presumably through unwonted nutrition, the sepals become exaggeratedly large, the petals remaining fairly typical for *W. fragarioides*." Teppner (1968) convincingly argued the opposite case, that the relative size of the sepals and petals are clearly shown and described, and this primary diagnostic characteristic between the two taxa should be taken at face value. A review of the description and plate (which serves as the type) confirms Teppner's opinion, making '*doniana*' the correct basionym for the southern taxon, should it be recognized taxonomically at the specific level. The plate in Sims (1813) (on which Trattinick's name is based) resembles Taxon B closely and obviously, in that it shows a plant with petals shorter than the sepals, a characteristic that is also stated in the text of both Sims (1813) and Trattinick (1823) as a distinctive or diagnostic characteristic. The stated provenance of the plant illustrated (Sims 1813) is pertinent, as well: "the plant, from which our drawing and description were taken, was brought from America, by Mr. Lyons [sic], and purchased at his sale, by Mr. Kent, of Clapton, by whom it was kindly communicated to us." Ewan & Ewan (1963) show that John Lyon listed this plant in a catalogue in 1812 (as

Dalibarda fragarioides), and also listed Mr. William Kent as having purchased plants for 14 £, 18 sh. in 1812. Presumably the plant illustrated the following year was in this lot. Though the location from which Lyon collected the plant cannot apparently be definitely known, the identification of John Lyon as the source of the plant illustrated and described is of interest, since Lyon collected extensively within the southeastern United States range of the small-petaled Taxon B. Thus, it seems very plausible that the plant described and figured as *Waldsteinia fragarioides* by Sims, and later described and named by Trattinick as the distinct *W. doniana*, is exactly what it appears to be.

Based on our review of generic circumscription, taxonomic distinctiveness, appropriate taxonomic rank, and nomenclature, we hereby effect the transfer of "Taxon B" to *Geum* at the rank of species:

Geum donianum (Tratt.) Weakley & Gandhi, comb. nov. *Waldsteinia doniana* Tratt., Rosacearum Monographia 3:109. 1823. Type: Curtis's Bot. Mag. 38: pl. 1567 (LECTOTYPE, designated here).

Waldsteinia parviflora Small, Bull. Torrey Bot. Club 25:137. 1898.

Waldsteinia fragarioides var. *parviflora* (Small) Fernald, Rhodora 37:285. 1935.

Waldsteinia fragarioides ssp. *doniana* (Tratt.) Teppner, Zur Kenntnis der Gattung *Waldsteinia*. Diss. Univ. Graz. 1968, nom. invalid., not effectively published under provisions of the ICBN Vienna Code (McNeill 2006). Article 30.5 states that "publication on or after 1 January 1953 of an independent non-serial work stated to be a thesis submitted to a university or other institute of education for the purpose of obtaining a degree is not effectively published unless it includes an explicit statement (referring to the requirements of the Code for effective publication) or other internal evidence that it is regarded as an effective publication by its author or publisher." Note 2 suggests forms of internal evidence as "the presence of an International Standard Book Number (ISBN) or a statement of the name of the printer, publisher, or distributor in the original printed version is regarded as internal evidence that the work was intended to be effectively published." Although Teppner distributed approximately 50 copies of his dissertation to botanical institutions and clearly intended this to constitute effective publication (H. Teppner, pers. comm., March 2008), we reluctantly conclude that he did meet the retroactive requirements of the Vienna Code, and therefore that there is currently no valid name for this taxon at the subspecific rank.

The taxa are distinguishable by the following key.

1. Leaves trilobed (the sinuses cleft 1/8 to 3/4 of the way to the midrib); petals shorter than to about as long as the sepals; first-year leaves rather densely pubescent with stiff hairs, these distributed on the veins and on the intervein surfaces; [of a small area at the southern terminus of the Southern Appalachians in n. GA, nw. SC, and sw. NC] ____ ***G. lobatum*** (Baldw.) Smedmark
1. Leaves trifoliolate (fully divided), and also typically additionally lobed; petals shorter than to longer than the sepals; first-year leaves sparsely pubescent with stiff hairs, these distributed mostly or strictly on the veins, the intervein surfaces glabrous to very sparsely pubescent; [more widespread].
   2. Petals 2.2–4 mm long (shorter then to about as long as the sepals), 1–1.5 mm wide; terminal leaflet with a distinct petiolule 1–6 mm long, the basal angle of the leaflet acute, mostly 60–90° (avg. 75°); [distributed in the Southern Appalachians and adjacent Piedmont of AL, GA, KY, NC, SC, and TN] ____ ***G. donianum*** (Tratt.) Weakley & Gandhi
   2. Petals 4–10 mm (longer than the sepals), 2–6 mm wide; terminal leaflet sessile or with a petiolule to 3 mm long, the basal angle of the leaflet about a right angle, mostly 75–105° (avg. 90°); [widely distributed in northeastern United States and adjacent Canada, south to VA, KY, and AR] ____ ***G. fragarioides*** (Michx.) Smedmark

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THE GENUS *ABRONIA* (NYCTAGINACEAE) IN COLORADO, WITH NOTES ON *ABRONIA BOLACKII* IN NEW MEXICO

Jennifer Ackerfield
Herbarium, Department of Biology
Colorado State University
Fort Collins, Colorado 80523, U.S.A.

William F. Jennings
P.O. Box 952
Louisville, Colorado, 80027, U.S.A.

ABSTRACT

Several taxonomic observations on the genus *Abronia* in Colorado and New Mexico are presented. First, *Abronia argillosa* Welsh & Goodrich is a synonym of *A. glabrifolia* Standl. Second, *Abronia carletonii* Coult. & Fisher is a synonym of *A. fragrans* Nutt. ex Hook., and specimens of *A. carletonii* from New Mexico and Texas should be called *A. nealleyi* Standl. Third, *Abronia elliptica* is a species distinct from *A. fragrans*, as noted by several fruit and habit characteristics. Lastly, recognition of the newly described *A. bolackii* appears unwarranted and should be included in synonymy under *A. elliptica*. A distribution map of *Abronia* in Colorado is presented as well as photographs of fruits of each species.

RESUMEN

Se presentan varias observaciones taxonómicas en el género *Abronia* en Colorado y Nuevo México. Primero, *Abronia argillosa* Welsh & Goodrich es un sinónimo de *A. glabrifolia* Standl. Segundo, *Abronia carletonii* Coult. & Fisher es un sinónimo de *A. fragrans* Nutt. ex Hook., y especimenes de *A. carletonii* de Nuevo México y Texas deben llamarse *A. nealleyi* Standl. Tercero, *Abronia elliptica* es una especie distinta de *A. fragrans*, como puede apreciarse por varias características del fruto y del hábito. Finalmente, el reconocimiento de la recientemente descrita *A. bolackii* parece injustificado y debería incluirse en la sinonimia de *A. elliptica*. Se presenta un mapa de distribución de *Abronia* en Colorado así como fotografías del fruto de todas las especies.

The Nyctaginaceae is a taxonomically complex family because of the heavy reliance upon mature fruit for identification (Galloway 2003; Welsh 2003). This is particularly true in the genus *Abronia*, where vegetative morphology can be highly variable within and among species while fruit morphology remains constant and distinct among taxa. The genus *Abronia* consists of 20 species, distributed throughout the Southwest, high Great Plains, Mexico, coastal California, and Pacific Northwest (Galloway 2003). Five species have been reported for the state of Colorado: *Abronia argillosa* Welsh & Goodrich, *A. carletonii* Coult. & Fisher, *A. elliptica* A. Nelson, *A. fragrans* Nutt. ex Hook., and *A. nana* S. Wats. var. *nana*. *Abronia bolackii* Atwood, Welsh & Heil is a newly described species endemic to San Juan County, New Mexico (Atwood et al. 2002).

Abronia argillosa is practically identical to *A. elliptica* vegetatively, and it is only through analysis of the fruit that identification can be made. Both species are perennial from a branching caudex with elliptic to ovate or suborbicular, entire leaves, and with white or purplish tinged flowers grouped in heads that are subtended by ovate to suborbicular bracts. However, *Abronia argillosa* has wingless fruit while *A. elliptica* has winged fruit with the wings dilated and inflated at the top (Fig. 1A,C). *Abronia argillosa* was described in 1980 (Welsh & Goodrich 1980) as a new species from Utah and Colorado restricted to Mancos Shale substrates. Examination of the original description of *Abronia glabrifolia* (Standley 1909) and the type specimen [Colorado: 1878, *Wm. F. Flint s.n.* (UC)] shows that this is clearly the same species. The type specimen of *A. glabrifolia* has the characteristic dark brown, wingless fruit with conspicuous white lines seen in the fruit of *A. argillosa* (Fig. 1C). The name *Abronia glabrifolia* predates that of *Abronia argillosa* by almost 70 years, and should thus be the name applied to all specimens of *A. argillosa*. William F. Flint was in Colorado at the Los Pinos Indian Agency in 1878 (Flint 1878), where he also collected a type specimen of *Senecio flintii* Rydb. [Colorado: S.W. Colorado, *Wm. F. Flint s.n.* (NY)]. Los Pinos was the name for the Ute Indian Agency, located about 25 miles north of Ouray and 11 miles south of Montrose, near the town of Eldredge (Young 1997), on what was then the reservation for the Uncompahgre Ute tribe. This locality is close to the Montrose-Ouray County line. Mancos Shale, the type of habitat known to support *A. glabrifolia* populations (Fig. 2), occurs in the vicinity.

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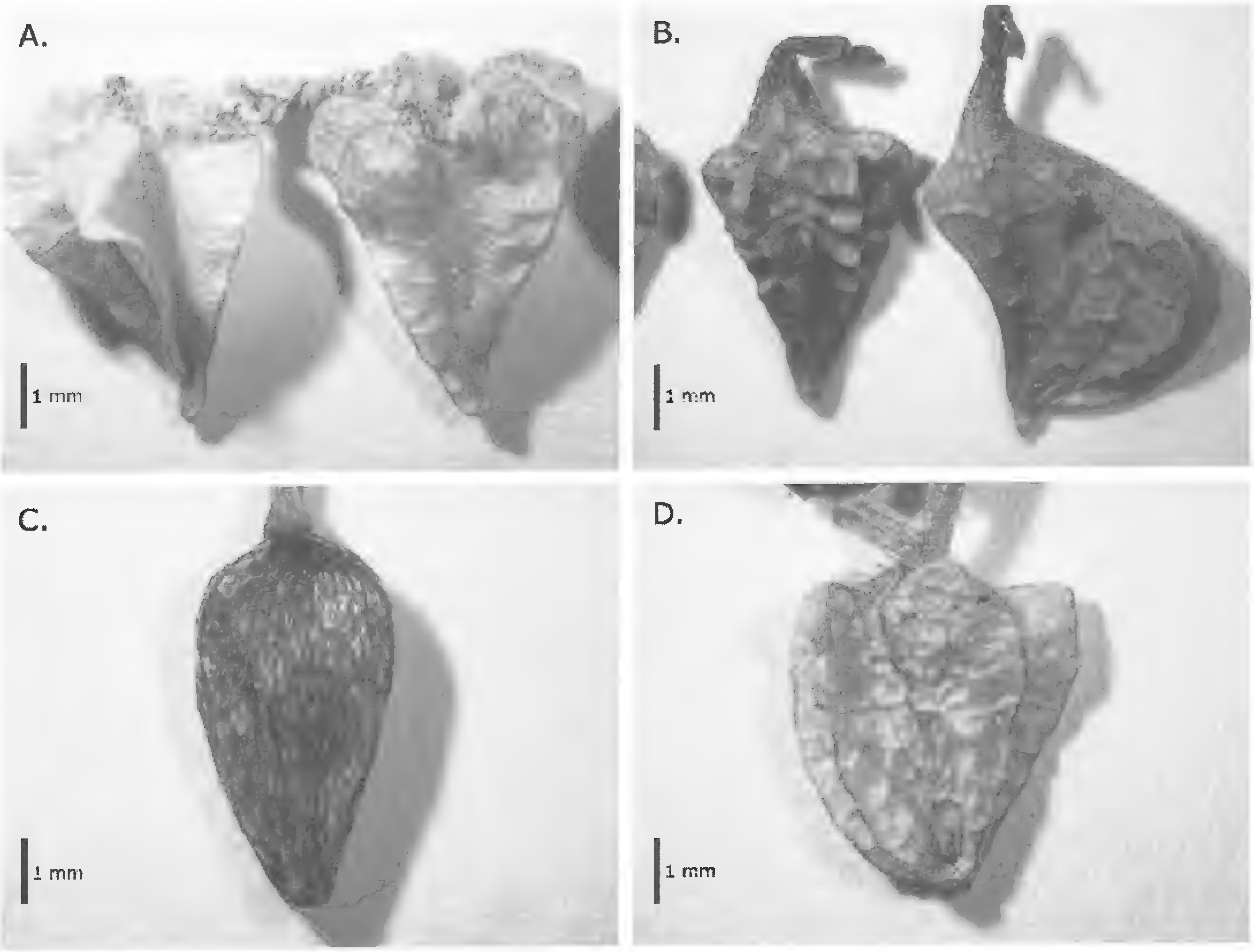

Fig. 1. ***Abronia*** **fruit (taken at 10×). A.** ***A. elliptica*** **[Colorado: Montrose Co.: Paradox Valley, Colo 90, 0.6 mi E of MP 20j. 3.8 mi E of junction with River Road; gypsum outcrop on S side of road, 22 May 2004,** ***Wm. F. Jennings s.n.*** **(CS)]. B.** ***A. fragrans*** **[Colorado: Yuma Co.: 30 mi S of Wray, 4 Aug 1948,** ***H.D. Harrington 4256*** **(CS)]. C.** ***A. glabrifolia*** **[Colorado: Garfield Co.: Wheeler Gulch, E end of Roan Plateau, 20 Jun 1981,** ***P Nicholas 53*** **(CS)]. D.** ***A. nana*** **var.** ***nana*** **[Colorado: Mesa Co.: Sinbad Valley, right fork of the road, 1.9 mi to barren gypsum hill on the N side of road 29.00, 27 May 2005,** ***Wm. F. Jennings s.n.*** **(CS)].**

The presence of *Abronia carletonii* in Colorado in particular has been questioned or misinterpreted by numerous taxonomists (Weber & Wittmann 2001). Assumption of its presence was based on the type collection made by Mark Carleton in 1891, and attributed to eastern Colorado. *Abronia carletonii* has not been collected in the state since, but is known to occur in New Mexico and Texas, where it is usually restricted to gypsum soil, very unlike the sandy soil that is found on the eastern plains of Colorado. Examination of the type specimen of *A. carletonii* [Colorado: Eastern Colorado, 1891, *M.A. Carleton 459*, (F)] confirms that it is actually a narrow-leaved, trailing form of *A. fragrans*. The fruit is winged, but the wings are not dilated and are thick and indurate as in typical *A. fragrans* (Fig. 1B). This form of *A. fragrans* is seen in other specimens from the plains growing in sandy soil [Colorado. Baca Co.: sand hills on south bank of Cimarron River, 31 Aug 1949, *Weber & Anderson 5157* (KANU); Kansas. Finney Co.: ca. 2.5 mi S Garden City, scattered in sand dune area south of Arkansas River, 11 Sep 1989, *Brooks & McGregor 19676* (KANU)]. In addition, the specimen was probably not collected in Colorado at all, but in extreme southwestern Kansas, just north of Elkhart, where the only *Abronia* known to be present is *A. fragrans*. The name *A. carletonii* should now be subsumed under *A. fragrans*, and specimens of *A. carletonii* in New Mexico and Texas should be referred to as *A. nealleyi* Standley, as suggested by Turner (2004).

In the Holzinger tabulation (Holzinger 1892), collection number 459 is not an *Abronia* at all, but is shown to be *Cnicus altissimus* and was collected in Kingfisher County, Oklahoma in August. The specimen

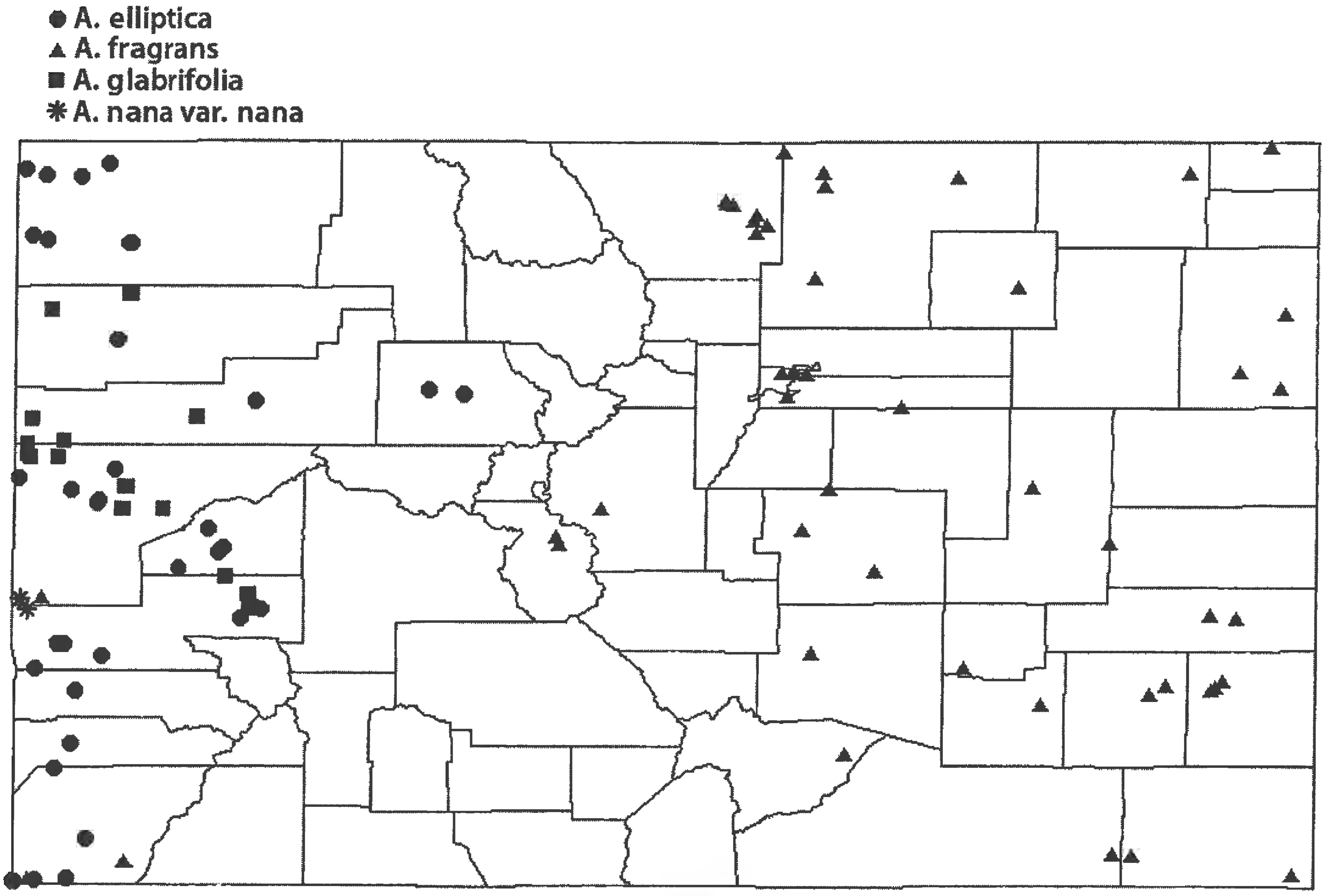

Fig. 2. Distribution of *Abronia* species in Colorado (based on herbarium specimens from CS and COLO). *A. elliptica* = circle; *A. fragrans* = triangle; *A. glabrifolia* = square; *A. nana* var. *nana* = star.

labeled collection number 459 of *Abronia carletonii* likely has the wrong label information, and is probably collection number 352 of *Abronia fragrans* collected in July in Morton County, Kansas, along the Cimarron River, probably near Point of Rocks north of Elkhart. According to Holzinger (1892), Carleton collected in Oklahoma, Kansas, and Texas, but not Colorado. Carleton began his collection trip in Oklahoma in June, collecting in the Cimarron Valley (collection numbers 202–235). He then continued north to Kansas where he collected until July (collection numbers 236–353), traveling across the southcentral counties of Comanche, Barber, Harper, and Sumner before going north to Sedgwick County. He continued westward from Wichita making collections in Reno and Stafford counties, and then in Seward, Stevens, and Morton counties in extreme southwestern Kansas. Carleton then traveled back to Oklahoma and Texas in July and August (collection numbers 354–474).

Some taxonomists consider *Abronia elliptica* to be synonymous with, or a variety of, *Abronia fragrans*. In particular, Welsh (2003) includes *A. elliptica* within a broad concept of *A. fragrans*. However, he misquotes Galloway (1975) as saying that the fruit of *A. elliptica* is 2-winged with a groove between the wings, and that of *A. fragrans* is 2–5-winged but not especially grooved. In fact, Galloway (1975) states that *A. elliptica* is 5-winged or 2-winged with the wings folded together, with dilated wing tops on the fruits that are not folded. Galloway (1975) further states that *A. fragrans* is deeply grooved or narrowly winged, with thick wings that are not inflated at the top. The fruits on the periphery of the heads in both *A. fragrans* and *A. elliptica* are often contorted, with 2 wings folded together, while the fruits in the middle of the head are 5-winged.

Careful analysis of the fruit as well as habit shows that *A. elliptica* and *A. fragrans* are indeed different species, as shown by the following characters. First, the fruit of *A. fragrans* is wingless or winged, with hard, rather indurate wings that are flat and lacking dilations (Fig. 1B). The fruit on the periphery of the heads is

often wingless in *A. fragrans* while within the central portion, fruits are winged. In contrast, *A. elliptica* has winged fruit with papery thin wings that are inflated and dilated at the top (Fig. 1A). Second, *A. fragrans* is generally a prostrate and spreading or semierect plant with more robust stems 3–5 mm wide, and with leaves that are ovate to triangular or lanceolate, especially on the upper part of the stem. *Abronia elliptica*, however, is generally erect or sometimes semierect with narrower stems typically 2–3 mm wide, with ovate to elliptic-oblong leaves. In addition, the distribution of *A. elliptica* in Colorado is scattered in the western counties. In contrast, *A. fragrans* is common on the eastern plains, but is also found in Chaffee County near Buena Vista. It is uncommon in the southwestern counties with a few records from Montezuma County and one from Mesa County (Fig. 2).

Abronia nana var. *nana* in Colorado is known only from gypsum outcrops in the Sinbad Valley in extreme western part of the state, on the Mesa-Montrose county line. This is the easternmost edge of its distribution range. It is a very distinctive species with acaulescent stems, and the entire plant is usually extremely viscid glandular. The fruit of *A. nana* var. *nana* is conspicuously viscid glandular and also winged. The five wings are broad, flat, and not dilated at the top (Fig. 1D).

Abronia bolackii Atwood, Welsh & Heil is a newly described species of *Abronia* endemic to gypsum soil in San Juan County, New Mexico (Atwood et al. 2002). It is delimited from *A. elliptica* based on the presence of rhizomes and fewer flowers per head (15–25 opposed to 25–75). However, the fruit and habit of *A. bolackii* are identical to that of *A. elliptica*. Specimens of *A. elliptica* with rhizomes have been collected as far north as San Juan County, Utah [Utah: San Juan Co.: E base of Comb Ridge just N of Hwy US 613, 1 Jun 1999, *L. Yeatts 4251* (COLO)]. Richard Spellenberg (pers. comments) has also observed rhizomatous *A. elliptica* plants throughout its range from northcentral Arizona and northwestern New Mexico to northeastern Utah and southwestern Wyoming, including western Colorado. Welsh (2003) states that recognition of the occasional rhizomatous plants (of *A. elliptica*, included within his description of *A. fragrans*) at any taxonomic level seems unwarranted. In addition, several specimens of *A. elliptica* have as few as 19–24 flowers per head [Colorado: Moffat Co.: ca. 2.5 mi E of mouth of Irish Canyon, 7 Jun 1983, *Baker & Kennedy 83-32* (CS); Colorado: Moffat Co.: Junction of Green and Yampa rivers, 8 Jul 1945, *H.D. Harrington 1480* (CS); Colorado: Mesa Co.: Rabbit Valley, sandstone outcrop in sandy soil, 21 May 2004, *Wm. F. Jennings s.n.* (CS)]. Finally, the range of *A. bolackii* is well within the range of *A. elliptica*. Consequently, the status of *A. bolackii* as a species appears unjustified, and should be included in synonymy under *A. elliptica*.

The following key includes the common name, scientific name, synonyms (if applicable), ecology and/or distribution, elevation range, flowering time, and occurrence on the eastern or western slope of Colorado (designated by an E or W, respectively) for each species.

KEY TO THE SPECIES OF *ABRONIA* IN COLORADO

1. Plants acaulescent, usually caespitose from a much-branched woody caudex; fruit extremely viscid and sticky glandular, with 5 broad wings that are flat and not dilated; leaves to 2.5 cm in length, conspicuously viscid glandular ____ **A. nana** S. Wats. var. **nana**

   DWARF SAND-VERBENA. Uncommon on gypsum outcrops in the Sinbad Valley, known in Colorado from Mesa and Montrose cos., 5400–5800 ft. Apr–May. W.

1. Plants caulescent, spreading and procumbent to erect; fruit unwinged or winged, dilated or flat, glabrous to villous or glandular at the top, but not conspicuously viscid; leaves 1.5–12 cm in length, glabrous to glandular, but not densely so.

   2. Fruit all wingless, dark brown to gray-brown with conspicuous small, appressed white lines but otherwise glabrous, and without a distinct reticulate vein pattern; flowers glabrous to sparsely glandular on the upper tube and lobes; bracts obovate to ovate or elliptic and rounded at the tips ____ **A. glabrifolia** Standl.

      CLAY SAND-VERBENA. [=*A. argillosa* Welsh & Goodrich]. Found on clay soil of the Mancos Shale formation, known in Colorado from Garfield, Mesa, Montrose, and Rio Blanco cos., 4700–6800 ft. May–Jun. W.

   2. Fruit usually winged or sometimes wingless on the periphery of the head, white, greenish, or tan or brown, sometimes with appressed white lines but these not pronounced, usually villous and/or glandular especially at the top, with a conspicuous reticulate vein pattern throughout; flowers sparsely to densely glandular

throughout; bracts ovate to obovate or elliptic with rounded or more often acuminate or mucronate tips.

3. Fruit winged or unwinged, the wings not dilated distally but flattened, thick and indurate, the peripheral fruit often curved in side view; plants spreading and procumbent to semierect; leaves ovate to triangular or sometimes narrow and lanceolate on the upper part of the stem; bracts ovate to linear-lanceolate, with acuminate tips ______ **A. fragrans** Nutt. ex Hook.

FRAGRANT SAND-VERBENA. Found in sandy soil, especially common on the eastern plains, but also known from a few collections in the southwestern counties (Mesa and Montezuma), 3500–8000 ft. May–Aug(–Sep). E/W.

3. Fruit winged, the wings dilated (inflated) and expanded distally, thin and papery; plants erect or somewhat spreading; leaves ovate, elliptic, or sometimes orbicular; bracts ovate to obovate, with rounded or acuminate tips ______ **A. elliptica** A. Nels.

WESTERN SAND-VERBENA. Found on gypsum, clay, or sandy soil, known in Colorado from the western counties (Delta, Dolores, Eagle, Garfield, Mesa, Moffat, Montezuma, Montrose, Ouray, Rio Blanco, and San Miguel), 4500–6500(–8200) ft. Apr–Jun. W.

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BOOK REVIEW

Nigel Smith, Rodolfo Vasquez, and Walter H. Wust. 2007. **Amazon River Fruits: Flavors for Conservation.** (ISBN 978-9972-2974-2-7, pbk.). Amazon Conservation Association, Missouri Botanical Garden Press, P.O. Box 299, St. Louis, Missouri 63166-0299, U.S.A. (**Orders:** www.mbgpress.org, mbgpress@mobot.org, 1-314-577-9534, 1-314-577-9594 fax). $35.00, 272 pp., color figures and photographs, 9.5" × 8".

Contents.—Preface, Acknowledgments, Introduction, Anacardiaceae, Annonaceae, Apocynaceae, Arecaceae, Celastraceae, Chrysobalanaceae, Clusiaceae, Combretaceae, Convolvulaceae, Costaceae, Dichapetalaceae, Euphorbiaceae, Fabaceae, Gnetaceae, Lecythidaceae, Malpighiaceae, Malvaceae, Melastomataceae, Memecylaceae, Menispermaceae, Moraceae, Muntingiaceae, Myrsinaceae, Myrtaceae, Olacaceae, Passifloraceae, Polygalaceae, Polygonaceae, Rubiaceae, Sapindaceae, Sapotaceae, Simaroubaceae, Solanaceae, Theophrastaceae, Urticaceae, Verbenaceae, Bibliography Notes, References, Photo credits.

This book attempts to woo its readers by commanding the attention of all their senses. The 1.4 lb soft cover book wrapped in a mixed matte and glossy cover weighs nicely in the hand, while photographs depicting colorful Amazonian fruits and a winding Amazonian river entertain the eyes. Past this pleasing explosion of color, an 11-page introduction discusses the location and rationale for research into wild edible fruits, mentioning the high diversity of such species in wetland communities and the threats of exploitation that these habitats face.

Over 100 species of edible fruit are described from wetland areas in and around the Pacaya-Samiria National Reserve in Northern Peru, representing only a fraction of the several hundred species of wild and domesticated fruits consumed by people in this region. Species accounts are organized by the botanical family to which they belong and follow a standard format throughout the book, with the scientific names listed at the top of the page and common name(s) listed below, organized by the country to which they pertain. Most accounts are allocated two pages in the book, with a full page devoted to photographs and the remainder of the space occupied by text.

Species accounts include a discussion of the natural history of the fruit, including distribution, phenology, pollination, and dispersal, as well as a history of its management as a resource. Fruit are discussed that have been under different levels of management, from those eaten only locally (e.g., *Psychotria loretensis*, Rubiaceae, "huanchaco huayo"), to those transported to local markets (e.g., *Passiflora nitida*, Passifloraceae, a relative of cultivated passionfruit), to those entering the international markets (e.g., *Theobroma cacao*, chocolate). Fruit descriptions are set in the context of their natural habitats and the need to make responsible choices about their cultivation, but encourage the search for emerging contributions to the world fruit choices.

The authors cater to a general naturalist audience that is interested in learning about Amazonian diversity and conservation through a readily accessible medium, one which they might easily relate to as they walk through a Peruvian marketplace. Species accounts are informative and contain sufficient information, leaving readers thirsting for more as they work through the book and gain a more complete understanding of both the environmental and cultural landscape in Amazonia.—*Tiana F. Franklin, M.S. Environmental Science, Botanical Data Specialist, Botanical Research Institute of Texas, 500 East 4th Street, Fort Worth, Texas 76102-4025, U.S.A.*

FURTHER TRANSFERS OF GLANDULAR-PUBESCENT SPECIES FROM *CHENOPODIUM* SUBG. *AMBROSIA* TO *DYSPHANIA* (CHENOPODIACEAE)

Sergei L. Mosyakin
M.G. Kholodny Institute of Botany
National Academy of Sciences of Ukraine
2 Tereshchenkivska Street, Kiev, 01601 UKRAINE

Steven E. Clemants
Brooklyn Botanic Garden
1000 Washington Ave.
Brooklyn, New York 11215 U.S.A.

ABSTRACT

The following new combinations in *Dysphania* are proposed for 21 species previously placed in *Chenopodium* subg. *Ambrosia*: **Dysphania melanocarpa** (J.M. Black) Mosyakin & Clemants, **D. pusilla** (Hook. f.) Mosyakin & Clemants, **D. truncata** (P.G. Wilson) Mosyakin & Clemants, **D. saxatilis** (P.G. Wilson) Mosyakin & Clemants, **D. andicola** (Phil.) Mosyakin & Clemants, **D. burkartii** (Aellen) Mosyakin & Clemants, **D. dunosa** (L.E. Simón) Mosyakin & Clemants, **D. oblanceolata** (Speg.) Mosyakin & Clemants, **D. retusa** (Juss. ex Moq.) Mosyakin & Clemants, **D. sooana** (Aellen) Mosyakin & Clemants, **D. tomentosa** (Thouars) Mosyakin & Clemants, **D. venturii** (Aellen) Mosyakin & Clemants, **D. bonariensis** (Hook. f.) Mosyakin & Clemants, **D. microcarpa** (Phil.) Mosyakin & Clemants, **D. nepalensis** (Colla) Mosyakin & Clemants, **D. procera** (Hochst. ex Moq.) Mosyakin & Clemants, **D. dissecta** (Moq.) Mosyakin & Clemants, **D. mandonii** (S. Watson) Mosyakin & Clemants, **D. stellata** (Standley) Mosyakin & Clemants, **D. congolana** (Hauman) Mosyakin & Clemants, and **D. minuata** (Aellen) Mosyakin & Clemants.

Key Words: Chenopodiaceae, *Chenopodium*, *Dysphania*, nomenclature, new combinations, taxonomy

RESUMEN

Se proponen las siguientes combinaciones nuevas en *Dysphania* para 21 especies previamente asignadas a *Chenopodium* subg. *Ambrosia*: **Dysphania melanocarpa** (J.M. Black) Mosyakin & Clemants, **D. pusilla** (Hook. f.) Mosyakin & Clemants, **D. truncata** (P.G. Wilson) Mosyakin & Clemants, **D. saxatilis** (P.G. Wilson) Mosyakin & Clemants, **D. andicola** (Phil.) Mosyakin & Clemants, **D. burkartii** (Aellen) Mosyakin & Clemants, **D. dunosa** (L.E. Simón) Mosyakin & Clemants, **D. oblanceolata** (Speg.) Mosyakin & Clemants, **D. retusa** (Juss. ex Moq.) Mosyakin & Clemants, **D. sooana** (Aellen) Mosyakin & Clemants, **D. tomentosa** (Thouars) Mosyakin & Clemants, **D. venturii** (Aellen) Mosyakin & Clemants, **D. bonariensis** (Hook. f.) Mosyakin & Clemants, **D. microcarpa** (Phil.) Mosyakin & Clemants, **D. nepalensis** (Colla) Mosyakin & Clemants, **D. procera** (Hochst. ex Moq.) Mosyakin & Clemants, **D. dissecta** (Moq.) Mosyakin & Clemants, **D. mandonii** (S. Watson) Mosyakin & Clemants, **D. stellata** (Standley) Mosyakin & Clemants, **D. congolana** (Hauman) Mosyakin & Clemants, y **D. minuata** (Aellen) Mosyakin & Clemants.

INTRODUCTION

The genus *Chenopodium* L. (Chenopodiaceae) in its traditional wide circumscription has long been suspected to be an unnatural (polyphyletic or paraphyletic) union of taxa belonging to different phylogenetic lineages. Consequently, many segregate genera and infrageneric taxa of various ranks were described and accepted within this group by various authors (see an overview in Scott, 1978). The genus *Dysphania* R. Br. during its turbulent taxonomic and nomenclatural history also experienced numerous shifts: from a single genus of a separate family Dysphaniaceae (Pax & Hoffmann 1934) or a representative of Illecebraceae or Caryophyllaceae—to a mere section of *Chenopodium* s.l. (Aellen 1930a, 1930b; see also discussion in: Eckardt 1967; Mabry & Behnke 1976; Scott 1978; Wilson 1983, 1984; Mosyakin & Clemants 2002, and references therein). The present article continues a series of our publications (Mosyakin 1993; Mosyakin & Clemants 1996, 2002; Clemants & Mosyakin 2003) on *Chenopodium* L. s.l. and its segregates.

Earlier (Mosyakin & Clemants 2002) we justified the transfer of species previously placed in *Chenopodium* L. subg. *Ambrosia* A.J. Scott, commonly called and henceforth referred to as glandular chenopods, to the genus *Dysphania*, and validated new taxonomic combinations in preparation for the treatment of the genus in *Flora of North America north of Mexico* (Clemants & Mosyakin 2003). At that time we made 18 new combinations, including 11 at the species level, 4 at the section level, and 3 at the level of subsection. Nomenclatural changes were essentially limited to taxa occurring in North America (both native and introduced), leaving a number of glandular chenopods yet to be formally transferred to *Dysphania*.

The taxonomic and nomenclatural decisions treating glandular chenopods within an expanded *Dysphania* were further discussed in the Dr. Sci. dissertation of Mosyakin (2003). The genus *Dysphania* circumscribed so as to include all glandular taxa of *Chenopodium* has been accepted for the treatments of *Chenopodiaceae* in *Flora of North America north of Mexico* (Clemants & Mosyakin 2003) and *Flora of China* (Zhu Gelin, Mosyakin & Clemants 2003). At least one additional transfer of a species from *Chenopodium* to *Dysphania* (*D. pdseudomultiflora* (Murr) Verloove & Lambinon) has been made (Verloove & Lambinon 2006) since then.

Here we validate new combinations in *Dysphania* for other species not transferred to that genus earlier. We refrain here from making specific conclusion on phylogenetic relationships within *Dysphania*. However, judging from a thorough analysis of relevant literature, our herbarium and field experience, studies of morphology and biogeography of glandular chenopods, we firmly believe that *Dysphania* in the new circumscription is a natural phylogenetic unit distinct from *Chenopodium* s.s. Since 2002 it was partly confirmed by molecular phylogenetic studies.

DISCUSSION

Results of recent molecular studies confirmed to some extent a deep phylogenetic split between at least three branches (clades) containing taxa previously traditionally placed in *Chenopodium* s.l. (Kadereit et al. 2003, 2005). Species of *Chenopodium* s.l. appeared scattered in three lineages informally named Chenopodieae I, II, and III. The segregation of species between these three clades mainly corresponded to recognized subgenera of *Chenopodium* s.l. (subgenera *Chenopodium*, *Blitum* (L.) I. Hiitonen, and *Ambrosia* A.J. Scott, respectively; see Scott, 1978). In particular, Kadereit et al. (2003, p. 976) indicated: "In Chenopodieae III, a close relationship of the Eurasian species *Chenopodium botrys* and *Teloxys aristata*, and of the Australian species *Chenopodium cristatum* and *Dysphania glomulifera*, is supported by the presence of multicelluar glandular hairs (type 8 in Carolin 1983). By that character, they fit into subgenus *Ambrosia* (Scott 1978; Simón 1996). <…> These results confirm the proposal of Mosyakin and Clemants (2002) to transfer *Chenopodium* subg. *Ambrina* [sic! – S. M. & S. C.] to *Dysphania* <…>." In a study of the origin and age of Australian Chenopodiaceae Kadereit et al. (2005, p. 74) indicated that "[r]ecently, Mosyakin and Clemants (2002) used morphological characters to separate subg. *Ambrosia* from *Chenopodium*, and included it in *Dysphania*. This last view is strongly supported by our results."

Other options alternative to our wide circumscription of *Dysphania* would be to recognize several genera, for example, *Teloxys* Moq. (including only *Chenopodium aristatum* L. = *T. aristata* (L.) Moq., or also other related taxa), *Roubieva* Moq. (mainly an American group, which may be recognized either in the original sense of Moquin-Tandon (1834), or with addition of other American taxa), the Australian group previously placed in *Chenopodium* sect. *Orthosporum* R.Br., and Australian *Dysphania* in its traditional circumscription. These groups, corresponding mainly to sections in various classification schemes of *Chenopodium* s.l., seem to be natural. However, recognition of such groups as genera, at least at our present level of knowledge, has its negative aspects related to paraphyly or yet uncertain phylogenetic positions of many taxa. In our opinion, a slightly expanded circumscription of *Dysphania* (including related sect. *Orthosporum*, but excluding other non-Australian taxa) would be also inconvenient, because it will erase practically applicable morphological diagnostic characters distinguishing the resulting broader genus from other glandular taxa.

For avoiding such problems and for maintaining the nomenclatural stability we strongly prefer to place all glandular chenopods in *Dysphania*, which is characterized by its glandular trichomes and also by other morphological and biochemical characters extensively discussed in literature (Scott 1978; Carolin 1983; Wilson 1983; 1984; Palomino et al. 1990; Schwarzová 1993; Simón 1995, 1996; Bonzani et al. 2003 etc.).

In the present article we validate 21 new nomenclatural combinations at the species level resulting from the transfers of glandular-pubescent species to *Dysphania*. A moderately narrow species concept is applied, which is mainly consistent with prevalent taxonomic treatments of "glandular chenopods" and species of *Chenopodium* s.l. We admit that many species of the considered groups are in need of further revisions and more detailed studies, but that should not preclude making available new combinations in *Dysphania* for

them. In addition to our experience and herbarium studies of these taxa, we especially consulted with and relied upon the basic taxonomic publications by Aellen (1930a, 1930b, 1933, 1973), Aellen and Just (1943), Wilson (1983, 1984, 1987), Simón (1995, 1996, 1997), as well as other relevant works (Voroshilov 1942; Scott 1978; Carolin 1983; Weber 1985; Palomino et al. 1990; Kühn 1993; Schwarzová 1993; Uotila 1997, 2001).

VALIDATION OF THE NEW COMBINATIONS

1. **Dysphania** sect. **Orthospora** (R. Br.) Mosyakin & Clemants, Ukrayins'k. Bot. Zhurn. 59:382. 2002.

Several names of putative hybrids between Australian taxa belonging to *Dysphania* sect. *Orthospora* were published (Aellen 1933, 1961; Wilson 1983, 1984). However, since their taxonomic status remains uncertain and their hybrid origin is mostly in need of confirmation, we refrain from making here any new combinations for hybrids.

Dysphania melanocarpa (J.M. Black) Mosyakin & Clemants, comb. nov. Basionym: *Chenopodium carinatum* R. Br. var. *melanocarpum* J.M. Black, Trans. & Proc. Royal Soc. South Australia 46:566. 1922. *Chenopodium melanocarpum* (J.M. Black) J.M. Black, Trans. & Proc. Royal Soc. South Australia 58:173. 1934.

Dysphania pusilla (Hook. f.) Mosyakin & Clemants, comb. nov. Basionym: *Chenopodium pusillum* Hook. f., Handb. New Zealand Fl. 1:231. 1864.

Dysphania truncata (P.G. Wilson) Mosyakin & Clemants, comb. nov. Basionym: *Chenopodium truncatum* P.G. Wilson, Nuytsia 4:177. 1983.

Dysphania saxatilis (P.G. Wilson) Mosyakin & Clemants, comb. nov. Basionym: *Chenopodium saxatile* P.G. Wilson, Nuytsia 4:179. 1983.

The last species was described by Wilson (1983) from Western Australia as *C. saxatile*. The author of the species noted that "[s]uperficially this species would appear to be related to the 4-merous species in the genus *Dysphania* (e.g. *D. rhadinostachya*) but in seed character it is obviously different, being very similar to *Chenopodium pumilio* and its allies of the section *Orthospora*. Yet even here its placement is uncertain since the other species of this section have flowers arranged in compact glomerules, have one stamen, and normally a 5-merous perianth." (Wilson 1983, p. 180). Wilson also compared his species with members of the *Chenopodium botrys* group (which evidently differ from *C. saxatilis* in having 5-merous perianth and horizontal seeds) and section *Margaritaria* (which has whitish subglobose, as well as glandular, hairs, and some other distinctive characters, see Brenan 1956), and concluded that "it appears that *C. saxatile* does not fit satisfactory into any of the presently recognized groups." P.G. Wilson refrained from describing a new monotypic section and instead expanded the circumscription of *Chenopodium* sect. *Orthosporum* to include his species. Pending further research, we keep the species in *Dysphania* sect. *Orthospora*.

2. **Dysphania** sect. **Adenois** (Moq.) Mosyakin & Clemants, Ukrayins'k. Bot. Zhurn. 59:382. 2002.

In our previous publications (Mosyakin & Clemants 2002; Clemants & Mosyakin 2003; Zhu Gelin et al. 2003) we mentioned that opinions vary widely regarding the proper species delimitation in this section, with some authors recognizing just a few species, including extremely polymorphic *Chenopodium ambrosioides* L. with infraspecific taxa, while other authors preferring several (up to 12) more narrowly circumscribed species (Aellen 1929, 1961, 1973; Aellen & Just 1943; Voroshilov 1942; Simón 1996, 1997; Giusti 1997). Sometimes the same author (notably Aellen) in different periods of his work was of differing opinions regarding the number of species related to *C. ambrosioides*. We believe that taxa in this group differ from each other not less than many generally recognized species of *Chenopodium* s.l. (subg. *Chenopodium*), especially in the *C. album* group. Numerous infraspecific entities were recognized in *C. ambrosioides* and some other variable taxa. In the present article we are concerned with the species-level taxonomy, and thus for the time being refrain from making any new infraspecific and infrageneric combinations.

Dysphania andicola (Phil.) Mosyakin & Clemants, comb. nov. Basionym: *Ambrina andicola* Phil., Anales Univ. Chile, I. Mem. Ci, Mem. Ci. Lit. 91:422. 1895. *Chenopodium ambrosioides* var. *andicola* (Phil.) Aellen, Feddes Repert. Spec. Nov. Regni Veg. 26:37. 1929.

Dysphania burkartii (Aellen) Mosyakin & Clemants, comb. nov. Basionym: *Chenopodium ambrosioides* L. subsp. *burkartii* Aellen, Feddes Repert. Spec. Nov. Regni Veg. 26:37. 1929. *Chenopodium burkartii* (Aellen) Vorosch., Bot. Zhurn. S.S.S.R. 27(3/4):46. 1942.

Dysphania dunosa (L.E. Simón) Mosyakin & Clemants, comb. nov. Basionym: *Chenopodium dunosum* L.E. Simón, Bull. Mus. Natl. Hist. Nat., B, Adansonia 10:407. 1988 [1989].

Dysphania oblanceolata (Speg.) Mosyakin & Clemants, comb. nov. Basionym: *Chenopodium ambrosioides* L. var. *oblanceolatum* Speg., Anales Mus. Nac. Hist. Nat. Buenos Aires 7:137. 1902. *Chenopodium oblanceolatum* (Speg.) Giusti in Correa, Fl. Patagonica (Colecc. Cient. 8) 4a:122. 1984.

Dysphania retusa (Juss. ex Moq.) Mosyakin & Clemants, comb. nov. Basionym: *Chenopodium retusum* Juss. ex Moq. in DC., Prod. 13(2):73. 1849.

Dysphania sooana (Aellen) Mosyakin & Clemants, comb. nov. Basionym: *Chenopodium sooanum* Aellen, Acta Bot. Acad. Sci. Hung. 19(1/4):5. 1973 (as "*sooianum*").

Dysphania tomentosa (Thouars) Mosyakin & Clemants, comb. nov. Basionym: *Chenopodium tomentosum* Thouars, Fl. Tristan d'Acugna 38. 1811.

Dysphania venturii (Aellen) Mosyakin & Clemants, comb. nov. Basionym: *Chenopodium ambrosioides* L. subsp. *venturii* Aellen in Aellen & Just, Amer. Midl. Naturalist 30:51. 1943. *Chenopodium venturii* Aellen ex Vorosch., Bot. Zhurn. S.S.S.R. 27(3/4):46. 1942 (invalid name: Russian description). *Chenopodium venturii* (Aellen) Cabrera, Revista Invest. Agric. 11:384. 1958.

3. **Dysphania** sect. **Roubieva** (Moq.) Mosyakin & Clemants, Ukrayins'k. Bot. Zhurn. 59:382. 2002.

Dysphania bonariensis (Hook. f.) Mosyakin & Clemants, comb. nov. Basionym: *Roubieva bonariensis* Hook. f. in Benth. & Hook. f., Gen. Pl. 3:52. *Chenopodium bonariense* (Hook. f.) Hauman & Irigoyen, Anales Mus. Nac. Hist. Nat. Buenos Aires 32:90. 1923, comb. illeg., non Ten. 1833. *Chenopodium haumanii* Ulbr. in Engl. & Prantl, Nat. Pflanzenfam. 16c:491. 1934.

Dysphania microcarpa (Phil.) Mosyakin & Clemants, comb. nov. Basionym: *Roubieva microcarpa* Phil., Anales Univ. Chile (Santiago), Mem. Cient. Liter. 91:423. 1895.

4. **Dysphania** sect. **Botryoides** (C.A. Mey.) Mosyakin & Clemants, Ukrayins'k. Bot. Zhurn. 59:383. 2002.

4a. **Dysphania** sect. **Botryoides** (C.A. Mey.) Mosyakin & Clemants subsect. **Botrys** (Aellen & Iljin) Mosyakin & Clemants, Ukrayins'k. Bot. Zhurn. 59:383. 2002.

The name of this subsection within the genus *Chenopodium* is often incorrectly cited as a combination *Chenopodium* subsect. *Botrys* (W.D.J. Koch) Aellen & Iljin. Since the name published by Koch is illegitimate, the above subsectional name should be attributed to Aellen and Iljin, who provided its description only in Russian, but also included a reference to the earlier pre-1935 publication and description by Koch, which makes their subsection validly published.

Dysphania nepalensis (Colla) Mosyakin & Clemants, comb. nov. Basionym: *Chenopodium nepalense* Colla, Herb. Pedemont. 5:571. 1836.

Chenopodium multiflorum Moq. in DC., Prodr. 13(2):75. 1849.

This little-known Central Asian species morphologically resembles *D. schraderiana* in its habit, but differs in having weakly keeled perianth segments with simple non-glandular hairs at the keel (Uotila 1993, 1997).

Another species closely related to *D. schraderiana* was recently transferred from *Chenopodium* to *Dysphania* as *D. pseudomultiflora* (Murr) Verloove & Lambinon (= *Chenopodium foetidum* Schrad. subsp. *pseudomultiflorum* Murr, *C. schraderianum* Schult. var. *pseudomultiflorum* (Murr) Aellen, *C. pseudomultiflorum* (Murr) Uotila) (Verloove & Lambinon 2006). Uotila (2001) indicated that this species of South African origin differs from

C. schraderianum in its more branched habit, leaves with more lobes and teeth, keeled but not cristate tepals with subsessile glands and long hairs, and smaller seeds.

Dysphania procera (Hochst. ex Moq.) Mosyakin & Clemants, comb. nov. Basionym: *Chenopodium procerum* Hochst. ex Moq. in DC. Prod. 13(2):75. 1849.

4b. **Dysphania** sect. **Botryoides** (C.A. Mey.) Mosyakin & Clemants subsect. **Incisa** (Standley) Mosyakin & Clemants, Ukrayins'k. Bot. Zhurn. 59:383. 2002.

Dysphania dissecta (Moq.) Mosyakin & Clemants, comb. nov. Basionym: *Ambrina dissecta* Moq., Chenop. Monogr. Enum. 38. 1840. *Chenopodium dissectum* (Moq.) Standley, N. Amer. Fl. 21:26. 1916.

Dysphania mandonii (S. Watson) Mosyakin & Clemants, comb. nov. Basionym: *Teloxys mandonii* S. Watson, Proc. Amer. Acad. Arts. Sci. 9:91. 1874 (as "*mandoni*"). *Chenopodium mandonii* (S. Watson) Aellen, Feddes Repert. Spec. Nov. Regni Veg. 26:169. 1929.

Chenopodium incisum Poir. var. *bangii* Murr, Bull. Herb. Boissier 4:991. 1904. *Chenopodium graveolens* Willd. var. *bangii* (Murr) Aellen, Verh. Naturf. Ges. Basel 41:107. 1931.

5. Taxa yet unplaced in sections of *Dysphania*

Dysphania stellata (Standley) Mosyakin & Clemants, comb. nov. Basionym: *Chenopodium stellatum* S. Watson, Proc. Amer. Acad. Arts Sci. 18:146. 1883. *Meiomeria stellata* (S. Watson) Standley, N. Amer. Fl. 21:7. 1916.

This morphologically deviant species having 6-8 perianth segments (described from Coahuila, Mexico) was placed by Standley (1916) in a separate genus *Meiomeria* Standley, and then transferred to *Chenopodium* sect. *Meiomeria* (Standley) A.J. Scott (Scott 1978). Relationships of this little-known taxon with other representatives of *Dysphania* remain insufficiently known.

Dysphania congolana (Hauman) Mosyakin & Clemants, comb. nov. Basionym: *Chenopodium glaucum* L. var. *congolanum* Hauman, Bull. Jard. Bot. État. Bruxelles 19:447. 1949. *Chenopodium congolanum* (Hauman) Brenan, Kew Bull. 11(1956):166. 1956.

Dysphania minuata (Aellen) Mosyakin & Clemants, comb. nov. Basionym: *Chenopodium minuatum* Aellen, Acta Bot. Acad. Sci. Hung. 19(1/4):8. 1973.

Dysphania congolana, an African species, was placed by Brenan (1956) in *Chenopodium* sect. *Margaritaria* Brenan, as *C. congolanum*; later Simón (1996) added *D. minuata* to this section (as *C. minuatum*).

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BOOK REVIEW

Robert W. Lebling and Donna Pepperdine. 2006. **Natural Remedies of Arabia.** (ISBN 9781905299027, hbk.). Stacey International Publishers, 128 Kensington Church Street, London, W8 4BH, United Kingdom. (**Orders:** www. stacey-international.co.uk, info@stacey-international.co.uk, +44 207 221 7166, +44 207 792 9288 fax). $55.00, 210 pp., color photographs, glossary, indexes, reference list, 10 3/4" x 12 1/2".

This book provides a wealth of information on the ethnobotany and pharmacognosy of the peoples of Saudi Arabia, Bahrain, Yemen, Oman, and the United Arab Emirates. It describes in detail 62 herbs, spices, oils, and minerals from the region, filling two to four pages per substance with factoids, historical nuggets, traditional uses, academic research notes, and family remedies. In particular, the family remedy portion for each plant was gleaned from "a questionnaire distributed throughout the Arabian Peninsula in 2002. The questionnaire...asked families to explain how they...use various herbs, spices and other substances in natural healing." Twenty-seven additional plants are also discussed but in much less detail and with few pictures.

The substances described in detail are: aloe vera, alum, anise, arak, arta, arugula, asafetida, banana, basil, black seed, caraway, cardamom, castor oil plant, chamomile, cinnamon, cloves, coffee, coriander, cress, cucumber, cumin, dates, fennel, fenugreek, frankincense, garlic, germander, ginger, hasawi rice, henna, herbal waters, hibiscus, honey, incense, lavender, lemon balm, lime, mahaleb cherry, mangrove, mastic, mint, myrrh, nakhwa, neem, nettle, petroleum, pomegranate, purslane, rose, saffron, sage, samh, sarcocol, sidr, tarthuth, thyme, desert truffles, turmeric, walnut bark, wormwood (sheeh), wormwood (bu'aythiran), and yarrow. The following are also described briefly: acacia, apple of Sodom, black nightshade, blond psyllium, caper, caralluma, cleome, colocynth, corn poppy, desert bugloss, dogbane, dwarf mallow, gum arabic, harmel, heliotrope, jericho rose, lemon grass, milkweed, myrtle, rat-tail plantain, safflower, senna, simple-leaved bean caper, smooth sow-thistle, spurge, tamarisk, and withania.

Immediately following the natural remedy descriptions is a Natural Beauty section that discusses Middle Eastern practices regarding natural hair care, skin care, and cosmetics, as well as uses for henna and mahaleb perfume. This section is presented in bullet form, with the text written in first person, presumingly drawn straight from the questionnaire responses mentioned above. A Recipes section is also included, with 29 pages of instructions for the preparation of traditional drinks, salads, soup, jam, dips, breakfast, desserts, main dishes, and spice mixtures, each using one or more of the previously discussed items.

The book concludes with the following sections: Glossary of Herbal Medicinal Terms, Index of Common Ailments, Bibliography & References, Index by Latin Name, and Index by Arabic Name. The Index of Common Ailments in particular serves as a handy quick reference to all the medical complaints addressed in the book.

All in all, *Natural Remedies of Arabia* was a delightful read from which I learned much about cultures far different than my own. If I ever have the privilege to travel in that part of the world, I will be sure to visit an herbal medicine shop to explore better in person this fascinating industry.—*M. Brooke Byerley, Botanical Research Institute of Texas, 500 East 4th Street, Fort Worth, Texas 76102-4025, U.S.A.*

NEW COMBINATIONS IN THE PANARCTIC VASCULAR PLANT FLORA

Reidar Elven

National Center of Biosystematics
Natural History Museum, University of Oslo
P.O.Box 1172 Blindern, NO-0318 Oslo, Norway
reidar.elven@nhm.uio.no

David F. Murray

University of Alaska Museum of the North
907 Yukon Drive
Fairbanks, Alaska 99775-6960, U.S.A.
ffdfm@uaf.edu

ABSTRACT

Thirty-eight new combinations are made in the families Asteraceae, Brassicaceae, Caryophyllaceae, Equisetaceae, Ericaceae, Fabaceae, Gentianaceae, Orchidaceae, Papaveraceae, Poaceae, Polygonaceae, Potamogetonaceae, Ranunculaceae, Rosaceae, and Saxifragaceae. The combinations are made so as to be available for the forthcoming Panarctic Flora Checklist.

RESUMEN

Se hacen treinta y ocho nuevas combinaciones en las familias Asteraceae, Brassicaceae, Caryophyllaceae, Equisetaceae, Ericaceae, Fabaceae, Gentianaceae, Orchidaceae, Papaveraceae, Poaceae, Polygonaceae, Potamogetonaceae, Ranunculaceae, Rosaceae, y Saxifragaceae. Las combinaciones se hacen para que estén disponibles en la próxima publicación de la Panarctic Flora Checklist.

A Panarctic Flora (PAF) Checklist Project has been in progress since 1999 (see Nordal & Razzhivin 1999) cooperatively among botanists with arctic interests in Canada, Iceland, Norway, Russia, and U.S.A. Its main aim is to produce a checklist of all arctic vascular plants with critical notes on distribution, chromosome numbers, and with proposals for accepted names based on consensus or compromises among participants. To reach a consensus nomenclature means harmonizing the different names and combinations currently applied in Russia, North America, and northwestern Europe. Alignment has meant new combinations requiring publication. The authors of new combinations are I. Alsos (Longyearbyen, Norway), R. Elven (Oslo, Norway), A.A. Korobkov (St. Petersburg, Russia), D.F. Murray (Fairbanks, U.S.A.), V.V. Petrovsky (St. Petersburg, Russia), O. Rebristaya (St. Petersburg, Russia), P. Schönswetter (Vienna, Austria), H. Solstad (Oslo, Norway), N.N. Tzvelev (St. Petersburg, Russia), and B.A. Yurtsev (St. Petersburg, Russia, deceased).

Equisetaceae

Equisetum arvense L. subsp. **alpestre** (Wahlenb.) Schönswetter & Elven, comb. et stat. nov. Basionym: *Equisetum arvense* L. var. *alpestre* Wahlenb., Fl. Lapp. 296. 1812. Type: N SCANDINAVIA ("Lapland"). Type not traced (Moberg & Nilsson 1991).

Equisetum boreale auct., non Bong., Mém. Acad. Imp. Sci. St.-Pétersbourg, Sér. 6, Sci. Math. 2:174. 1833. *Equisetum arvense* L. var. *boreale* auct., non (Bong.) Rupr., Hist. Stirp. Fl. Petrop. 91. 1845. *Equisetum arvense* L. subsp. *boreale* auct., non (Bong.) Á. Löve, Náttúrufrædingurinn 18:101. 1948.

An arctic–alpine race of *Equisetum arvense* L. has in recent years been accepted as subsp. *boreale* (Bong.) Á. Löve (e.g., by Öllgaard 2000). Schönswetter et al. (2001) argued that the name "*boreale*" is misapplied for the race in question. It is based on a Bongard plant from Sitka in southeastern Alaska representing a morph within subsp. *arvense*, differing from the arctic and high alpine plants in many morphological features. The next available name is Wahlenberg's var. *alpestre*, and a combination as subspecies is proposed here.

Potamogetonaceae

Stuckenia filiformis (Pers.) Börner subsp. **borealis** (Raf.) Tzvelev & Elven, comb. nov. Basionym: *Potamogeton borealis* Raf., Med. Repos., ser. 2, 5:354. 1808. Type: CANADA: Quebec: St. Lawrence R, *Michaux* (holotype: P). *Potamogeton filiformis* Pers. var. *borealis* (Raf.) H. St. John, Rhodora 18:134. 1916.

Stuckenia filiformis (Pers.) Börner subsp. *alpina* auct., non (Blytt) R.R. Haynes, Les & M. Král, Novon 8:241. 1998.

Northern North American plants of *Stuckenia filiformis* (Pers.) Börner differ from the main race by their broader leaves and more congested inflorescences. Such plants have been considered by authors (e.g., Hul-

tén 1968a; Cody 1996, 2000) as subsp. or var. *borealis*, based on Rafinesque's *Potamogeton borealis* from the St. Lawrence River region. Les and Haynes (1996) synonymized *Potamogeton borealis* with the Norwegian *Potamogeton marinus* L. f. *alpinus* Blytt, Norges Fl. 1:370 (1861), described from southern Norway, and they raised f. *alpina* to subspecific rank as the accepted name for the North American subspecies. Haynes et al. (1998) transferred *Potamogeton filiformis* to the genus *Stuckenia*, which we accept. Haynes and Hellquist (1998) reported subsp. *alpina* as restricted to North America and perhaps northeastern Asia, in spite of it being described from Norway.

Blytt's f. *alpinus* has not been lectotypified. The syntypes (O!) from the six sites listed in the protologue are all from southern Norwegian mountain valleys. They have not been studied by Les, Haynes or Hellquist. Les and Haynes (1996: 390) stated, when they synonymized Norwegian *'alpina'* and North American *'borealis'*, with priority for the former, that they had not seen type material (P) of *'borealis'*. Neither have we, but when we compare the syntypes of Blytt's Norwegian f. *alpinus* with North American plants, we find them different. We consider the Norwegian plants as montane–alpine modifications of European *Stuckenia filiformis* and not as an acceptable race (subspecies), whereas we consider the North American plant an acceptable race. We therefore propose to retain the North American name "*borealis*" for the northern North American plants. This taxon is characterised by two differential characters as given by Haynes and Hellquist (for subsp. *filiformis* vs. subsp. *alpina*, slightly modified here): leaves 0.2–0.4 mm vs 0.5–0.8(–1.0) mm broad, and infrutescence strongly interrupted and extending up to 4 cm vs more compact to somewhat interrupted and extending only up to 2 cm.

Orchidaceae

In the Panarctic Flora Checklist we accept *Limnorchis* Rydb. and *Lysiella* Rydb. as genera different from *Platanthera* Rich. We know of no thorough phylogenetic study of the *Platanthea* group, but in a study of Orchidinae and some Habenariinae, Bateman et al. (2003) found *Platanthera (Limnorchis) hyperborea* as peripheral to the main group of *Platanthera* spp. Acceptance of *Limnorchis* necessitates two new combinations:

Limnorchis aquilonis (Sheviak) Rebrist. & Elven, comb. nov. Basionym: *Platanthera aquilonis* Sheviak, Lindleyana 14:193. 1999.

Limnorchis huronensis (Nutt.) Rebrist. & Elven, comb. nov. Basionym: *Orchis huronensis* Nutt., Gen. N. Amer. Pl. 1:288. 1818. *Platanthera huronensis* (Nutt.) Lindl., Gen. Sp. Orchid. Pl. 288. 1835.

Poaceae

Calamagrostis purpurascens R. Br. subsp. **laricina** (Louis-Marie) Elven, comb. et stat. nov. Basionym: *Calamagrostis purpurascens* R. Br. var. *laricina* Louis-Marie, Rev. Oka Agron. Inst. Agric. 20:153. 1946. Type: CANADA: Quebec: Ungava, Riviere aux Melezes (Larch R), 57°42'N, 68°25'W, *Dutilly & Lepage 14602* (holotype: CAN). *Calamagrostis laricina* (Louis-Marie) Louis-Marie, Naturaliste Canad. 85:70. 1958.

Calamagrostis poluninii T.J.Sørensen, Meddel. Grønland 136, 8:11. 1954. Type: GREENLAND: Kiagtut in Tunugdliarfik, 15 Jul 1947, *Sørensen 188* (holotype: C).

Greene (1980, 1984) recognized two races in the very widespread *Calamagrostis purpurascens*: var. *purpurascens* from northern Siberia to northern Greenland (and recently found also on Svalbard) and var. *laricina* restricted to northeastern Canada and southern and western Greenland. The latter race is characterized by being short-rhizomatous and by having awns not distinctly exserted from the spikelet. Sørensen's description of *C. poluninii* in 1954 was made without reference to (and probably while unaware of) Louis-Marie's earlier description of var. *laricina* in 1946. Greene seems to have been the first to compare the types and recognize that the two names apply to the same plant.

The southern and western Greenland plants named *C. poluninii* are an extension of the northeastern North American *C. purpurascens* var. *laricina*. As this is a major geographical race, the rank of subspecies is preferable to variety, and a new combination is proposed.

Koeleria pyramidata (Lam.) P. Beauv. subsp. **seminuda** (Trautv.) Elven, comb. nov. Basionym: *Koeleria cristata* Pers. var. *seminuda* Trautv., Trudy Imp. S.-Peterburgsk. Bot. Sada 5, 1 [Pl. Sib. Bor.]:138. 1877. Type: SIBERIA: northern Sakha (Yakutia),

"Ad Lena inf. prope pag. Ajakit," 28 Jul 1875, *Czekanovski* (LECTOTYPE: LE, designated by Tzvelev, Zlaki SSSR 276. 1976.). *Koeleria seminuda* (Trautv.) Gontsch. in Kom., Fl. URSS 2:331. 1934. *Koeleria cristata* Pers. subsp. *seminuda* (Trautv.) Tzvelev, Novosti Sist. Vyssh. Rast. 7:71. 1971.

Koeleria cristata is an illegitime, superfluous name and must be replaced by *K. pyramidata* (Lam.) P. Beauv. *Koeleria seminuda* is here recombined as a subspecies within *K. pyramidata*.

Puccinellia phryganodes (Trin.) Scribn. & Merr. subsp. **neoarctica** (Á. Löve & D. Löve) Elven, comb. et stat. nov. BASIONYM: *Phippsia neoarctica* Á. Löve & D. Löve, Bot. Not. 128:499. 1976. TYPE: GREENLAND: Sydostbugt, Jul 1880, *N. Hartz* (HOLOTYPE: C). *Puccinellia neoarctica* (Á. Löve & D. Löve) Böcher et al., Grønlands Fl., ed. 3:293. 1978 [without basionym citation]. *Puccinellia phryganodes* (Trin.) Scribn. & Merr. "Greenland type" sensu Sørensen (1953).

Within the polymorphic, circumpolar *Puccinellia phryganodes*, Sørensen (1953) informally named four entities as "types": a fertile, tetraploid "Beringian type" ($2n = 28$) and three asexual types: a triploid "Greenland type" also widespread in arctic North America ($2n = 21$), a tetraploid "Spitsbergen—Novaya Zemlya type" restricted to these islands, and a "Siberian type" ranging from northeastern Norway (triploid) through arctic Russia and Siberia to Chukotka (tetraploid). Sørensen (1953) demonstrated anatomical and morphological differences in addition to the ploidy differences. We prefer to consider Sørensen's types major geographical races, i.e., subspecies, of a morphologically coherent species *phryganodes*. Subsp. *neoarctica* is a sterile stoloniferous race that reproduces by detached shoots.

Puccinellia phryganodes (Trin.) Scribn. & Merr. subsp. **sibirica** (Hadač & Á. Löve) Elven, comb. nov. BASIONYM: *Puccinellia vilfoidea* (Andersson) Á. Löve & D. Löve subsp. *sibirica* Hadač & Á. Löve in Á. Löve & D. Löve, Bot. Not. 114:36. 1961. TYPE: RUSSIA: "Waigatsch, Sinus Warnek," 14 Jul 1907, *O. Ekstam* (HOLOTYPE: S). *Phippsia vilfoidea* (Andersson) Á. Löve & D. Löve subsp. *sibirica* (Hadač & Á. Löve) Á. Löve & D. Löve, Bot. Not. 128:501. 1976. *Puccinellia phryganodes* (Trin.) Scribn. & Merr. subsp. *asiatica* Tzvelev in Tolm., Fl. Arct. URSS 2:186. 1964 [in error for "*sibirica*"]. *Puccinellia phryganodes* (Trin.) Scribn. & Merr. "Siberian type" sensu Sørensen (1953).

Tzvelev (1964) made a mistake in the basionym, replacing "*sibirica*" with "*asiatica*" when publishing *Puccinellia phryganodes* subsp. *asiatica*. At the rank of subspecies, the epithet "*sibirica*" (Hadač & Löve in Löve & Löve 1961) has priority over "*asiatica*" (Tzvelev 1964).

Vahlodea latifolia (Hook.) Hultén subsp. **paramushirensis** (Kudô) Elven, comb. nov. BASIONYM: *Deschampsia atropurpurea* (Wahlenb.) Scheele var. *paramushirensis* Kudô, J. Coll. Agric. Hokkaido Imp. Univ. 11:71. 1922. TYPE?: JAPAN: Paramushir I, Urafutoyama, 1920, *Kudô 5787*. *Vahlodea atropurpurea* (Wahlenb.) Fr. ex Hartm. subsp. *paramushirensis* (Kudô) Hultén, Fl. Kamtchatka 1:111. 1927. *Vahlodea paramushirensis* (Kudô) Roshev. in Kom., Fl. URSS 2:242, 750. 1934.

Erioblastus flexuosus Honda, J. Fac. Sci. Univ. Tokyo, sect. 3, Bot. 1:143. 1930. Described from Japan. *Vahlodea flexuosa* (Honda) Ohwi, Acta Phytotax. Geobot. 2:33. 1933.

The small genus *Vahlodea* (a segregate of *Deschampsia*) is disjunct in three very distant regions: around the North Atlantic, the northern Pacific, and in southernmost South America. From one to four species or subspecies have been proposed. Tzvelev recognized, besides the South American *V. magellanica* (Hook. f.) Tzvelev, three northern species: *V. atropurpurea*, *V. latifolia* and *V. flexuosa*. The amphi-Atlantic *V. atropurpurea* s. str. is fully allopatric with the two Pacific entities and differs morphologically from both of them. The most evident difference between the mainly northeastern Asian plant (*V. flexuosa* or *V. paramushirensis*) and the northwestern North American one (*V. latifolia*) is that the Asian plant has hairy leaves and the North American plant has glabrous leaves. They also differ in general habit, but there are many intermediates, especially in southern Alaska. Soreng et al. (2003) recognized only one species with two subspecies: subsp. *atropurpurea* (including both *V. latifolia* and the South American *V. magellanica*) and subsp. *paramushirensis*. The solution chosen for the Panarctic Flora Checklist is two northern species: one amphi-Atlantic (*V. atropurpurea*) and one amphi-Pacific (*V. latifolia*), the latter with two subspecies (subsp. *latifolia* and subsp. *paramushirensis*) inasmuch as the entities intergrade. This necessitates the new combination.

Polygonaceae

Bistorta elliptica (Willd. ex Spreng.) V.V. Petrovsky, D.F. Murray & Elven, comb. nov. BASIONYM: *Polygonum ellipticum*

Willd. ex Spreng., Syst. Veg. 2:253. 1825. Described from eastern Siberia. *Polygonum bistorta* L. subsp. *ellipticum* (Willd.) V.V. Petrovsky in Tolm., Fl. Arct. URSS 5:176. 1966. *Bistorta major* Gray subsp. *elliptica* (Willd.) Soják, Preslia 46:152. 1974.

The widespread *Bistorta officinalis* Delarbre s. lat. is disjunct montane and arctic. The northern montane and arctic plants differ from non-arctic European *Bistorta officinalis* s. str. in several characters, and they should be accepted as different race(s) or species. Freeman and Hinds (2005) accepted the northwestern North American and northeastern Asian plant as *B. plumosa* (Small) Greene. Petrovsky (1966), treating the plants for arctic Russia as races of *Polygonum bistorta*, assigned the plants from northeastern Europe and northern Siberia (Taimyr) to subsp. *bistorta* (= subsp. *officinalis*) and those from northeastern Siberia (Anabar–Olenyok) to the Chukchi Peninsula to subsp. *ellipticum*. He considered the North American subsp. *plumosa* as different from both of these. We agree with this division of the arctic Russian material but not with the application of the names. Tzvelev and Yurtsev (pers. comm.) assumed the "*elliptica*" name to belong to the western entity. *Polygonum ellipticum* was described from non-arctic parts of the Lena River area. In the Arctic, the limit between the western and the eastern entities runs through the Taimyr, but further south in Siberia and the Russian Far East this otherwise western arctic entity occurs in the mountains all the way eastward to the Okhotsk Sea. We therefore recombine *Polygonum ellipticum* within *Bistorta* and accept it as the name for the northern Russian and northwest Siberian plant. We consider the northeast Siberian and northern Russian Far East plants as indistinguishable from the North American *Bistorta plumosa*, in spite of a suggested difference in chromosome numbers.

Caryophyllaceae

Silene involucrata (Cham. & Schltdl.) Bocquet subsp. **furcata** (Raf.) V.V. Petrovsky & Elven, comb. et stat. nov. Basionym: *Silene furcata* Raf., Autik. Bot. 28. 1840. Type: CANADA: Hudson Bay–Labrador area: type not located. *Melandrium furcatum* (Raf.) Hultén, Acta Univ. Lund., n. s., sect. 2, 40, 1:702. 1944. [printing date not given, but probably early 1944] or: (Raf.) Hadač, Skr. Svalbard Nordishavet 87:34. 1944. [printed 04 May 1944]. *Gastrolychnis furcata* (Raf.) Hultén, Acta Univ. Lund., n.s., sect. 2, 40, 1:702. 1944. [comb. illegit].

Silene involucrata (Cham. & Schltdl.) Bocquet is a polymorphic species. We recognize it with three major races, a northern European—northwestern Siberian subsp. *tenella* (Tolm.) Bocquet, a northeastern Siberian—northwestern North American subsp. *involucrata*, and an arctic circumpolar subsp. *furcata*. Bocquet (1967) included both the boreal northern European and northwestern Siberian plants and the arctic circumpolar plants within *Silene involucrata* subsp. *involucrata*, an approach followed by Kurtto (2001) and Morton (2005). We find the races distinct at the level of subspecies. In three areas of co-occurrence (in the lower Lena River area of northern Siberia, in eastern Chukotka, and in northern Alaska—northwestern Canada) they are fully distinct in nature. Subspecies *furcata* then becomes the most widespread of the races. *Silene furcata* Raf. is not typified, but this race is the only one present in the Hudson Bay—Labrador area from where it was described. A subspecific combination based on this name is proposed. This was also the opinion of Tzvelev (2000).

Silene soczavana (Schischk.) Bocquet var. **macrosperma** (A.E. Porsild) V.V. Petrovsky, D.F. Murray & Elven, comb. et stat. nov. Basionym: *Melandrium macrospermum* A.E. Porsild, Rhodora 41:225. 1939. Type: ALASKA: Norton Sound, Unalakleet, 63°52'N, 106°20'W, *A.E. Porsild & R.T. Porsild 1147* (holotype: CAN). *Lychnis macrosperma* (A.E. Porsild), J.P. Anderson, Iowa State Coll. J. Sci. 20:250. 1946. *Silene macrosperma* (A.E. Porsild) Hultén, Circumpolar Pl. 2:326. 1971. *Gastrolychnis macrosperma* (A.E. Porsild) Tolm. & Kozhanch. in Tolm., Fl. Arct. URSS 6:115. 1971. *Silene uralensis* (Rupr.) Bocquet subsp. *porsildii* Bocquet, Candollea 22:27. 1967. Nomen novum for *Melandrium macrospermum* A.E. Porsild.

Bocquet (1967) treated Porsild's *Melandrium macrospermum* as subsp. *porsildii* of the widespread *Silene uralensis*, as a central Alaskan mountain endemic, whereas he accepted the northeastern Asian *Silene soczavana* as a separate species. The tetraploid chromosome number, morphology, ecology, and geography support inclusion of *M. macrosperma* within *S. soczavana*, not within *S. uralensis*. According to the material we have inspected, *Silene soczavana* var. *macrosperma* is a widespread taxon from eastern Chukotka and the northern Bering Sea islands northeast to the Alaskan North Slope and south and southeast to Kodiak Island and northern British Columbia.

Silene villosula (Trautv.) V.V. Petrovsky & Elven, comb. nov. Basionym: *Lychnis ajanensis* Regel var. *villosula* Trautv., Acta Horti Petrop. 10:498. 1887. Type: RUSSIA: northern Sakha (Yakutia), "ostia fl. Lena, Tonoldo [??]," *Köl. [Koelreuter?] 4711* (LE). *Lychnis sibirica* L. subsp. *villosula* (Trautv.) Tolm., Trudy Polyarn. Komiss. 8:118. 1932. *Sofianthe villosula* (Trautv.) Tzvelev, Novosti Sist. Vyssh. Rast. 33:97. 2001.

The evidence of Oxelman et al. (2001) strongly supports inclusion of the *Lychnis sibirica* L. group in *Silene*. This group contains three named entities that reach the Arctic (and some more southern entities). Oxelman et al. (2001) accepted two of them as species: *Silene linnaeana* Vorosch. and *S. samojedora* (Sambuk) Oxelman. They did not consider the third entity, *"villosula,"* in their analysis. Oxelman (pers. comm.) is open to accepting *"villosula"* as a third species. Tzvelev (2001) had already treated the three entities as species, but in the genus *Sofianthe*.

Silene violascens (Tolm.) V.V. Petrovsky & Elven, comb. nov. Basionym: *Gastrolychnis violascens* Tolm., Fl. Arct. URSS 6:115. 1971. Type: RUSSIA: Sakha (Yakutia), "ad flumen Daaldyn, in ditione fluminis Marcha, fluminis Viluj confluentis," 16 Jul 1957, *A. Lukitcheva* (holotype: LE?).

?*Lychnis uniflora* Ledeb., Mém. Acad. Imp. Sci. St. Pétersbourg Hist. Acad. 5:536. 1815. Type: RUSSIA: "Herb. Ledeb. In Sibiria transbaicalensi, lect. am. Tilesius" (holotype: LE!). ?*Gastrolychnis uniflora* (Ledeb.) Tzvelev, Bot. Zhurn. (Moscow & Leningrad) 85(11):101. 2000.

Silene violascens is related to *S. uralensis* but differs in morphology, habitat, and range. It is mainly a Siberian forest species. It is here recombined within *Silene* as the evidence of Oxelman et al. (2001) makes it very difficult to retain the genus *Gastrolychnis*. We also consider the type of *Gastrolychnis uniflora* (*Lychnis uniflora*), which Tzvelev (2000) considered a priority name for *Gastrolychnis uralensis*, a small plant of *S. violascens*. This will not influence priority in *Silene* as there is an earlier *S. uniflora* Roth 1794.

Ranunculaceae

Coptidium × spitsbergense (Hadač) Elven, comb. nov. Basionym: *Ranunculus x spitsbergensis* Hadač, Stud. Bot. Cech. 5:3. 1942. Type: NORWAY: Svalbard, Longyearbyen, 16 Jul 1939, *E. Hadač 260* (holotype: O).

Ranunculus pallasii Schltdl. var. *minimus* Rupr., Fl. Samojed. Cisural. 18. 1845. Type: RUSSIA: northeastern European Russia.

Ranunculus pallasii Schltdl. var. *spetsbergensis* Nath., Kongl. Svenska Vetenskapsakad. Handl., n.s., 20, 6:21. 1883. Type: NORWAY: Svalbard.

Coptidium (*Ranunculus*) *spitsbergense* is a seed-sterile triploid hybrid *Coptidium lapponicum* x *pallasii*. On Svalbard, from where it was first described, it occurs fairly frequently in large stands and nearly always in the absence of one or both parents (*C. pallasii* is very rare on Svalbard). It is obviously not a case of occasional hybridisation. Dispersal is assumed to be mainly or entirely by shoot fragments carried by birds. The identification with Ruprecht's var. *minimus* was made by Tolmachev (1971).

Hadač's *Ranunculus spitsbergensis* was not explicitly based on Nathorst's var. *spetsbergensis* and was given with a separate type. Nathorst's name, spelling and type have priority for a variety, whereas Hadač's name, spelling and type have priority for a species, see Jalas (1988). The combination *Coptidium* × *spitsbergense* (Hadač) Hadač in Á. Löve & D. Löve, North Atlantic Biota and their History 218 (1963), is illegitimate as the genus *Coptidium* was not validly published until 1994.

Ranunculus subborealis Tzvelev subsp. **pumilus** (Wahlenb.) Elven, comb. nov. Basionym: *Ranunculus acris* L. var. *pumilus* Wahlenb., Fl. Suec. 1:351. 1824. Type: SWEDEN: Lycksele lappmark, "Sorsele, at Ruopsokjaure," 03 Aug1948, *O. Rune 200/48* (neotype: UPS, designated by Nurmi in Jonsell, Nordic J. Bot. 20:520. 2001, according to Moberg and Nilsson 1991:298, no original material is available for typification). *Ranunculus acris* L. subsp. *pumilus* (Wahlenb.) Á. Löve & D. Löve, Taxon 34:164. 1985. ?*Ranunculus lanuginosiformis* Selin ex Trautv., Increm. Fl. Phaenog. Ross. 1:21. 1882.

We accept *Ranunculus subborealis* Tzvelev (the name replacing *R. borealis* Turcz. in a northern context) as a species separate from *R. acris* L.

There can be two different interpretations of the name *"pumilus"* and two different meanings derived from them. The older meaning is Nordic and based on *Ranunculus acris* var. alpha Wahlenb. 1811, formalized as *R. acris* var. *pumilus* Wahlenb. 1824. Nurmi's typification assigns this name to a Scandinavian alpine subglabrous race more closely related to *R. subborealis* than to *R. acris*. Intermediates are frequent between subsp. *pumilus* and other races of *R. subborealis* but not between subsp. *pumilus* and *R. acris*.

The other meaning is Russian and based on *R. acris* var. *pumilus* "Wahlenb. ex" J. Fellm., Bull. Soc. Naturalistes Moscou 8:271. 1835. If Fellmann really based his variety on Wahlenberg's var. alpha, then it is homotypic and a superfluous combination antedated by Wahlenberg 1824. Thus the Nordic meaning as established by the typification of Nurmi is also valid for Fellmann's variety. If not, var. *pumilus* sensu Fellmann is a later homonym. From the descriptions in several Russian floras, the application of the name var. *pumilus* J. Fellm. in Russian areas is different from that of the name var. *pumilus* Wahlenb. in Nordic areas.

Ranunculus subborealis Tzvelev subsp. **villosus** (Drabble) Elven, comb. et stat. nov. Basionym: *Ranunculus acris* L. f. *villosus* Drabble, Bot. Soc. Exch. Club Brit. Isles 9:472. 1930. *Ranunculus acris* L. subsp. *borealis* (Regel) Nyman var. *villosus* (Drabble) S.M. Coles, Watsonia 8:240. 1971.

This race connects morphologically with *Ranunculus subborealis* s. str. in northeastern Fennoscandia, with transitions in the Norwegian provinces of Troms and Finnmark and in northern Sweden and Finland. Transitions towards *R. acris* s. str. are rare. Subspecies *villosus* is the dominant entity of the *R. acris* group in the Faeroes and Iceland and a major entity in western and northern Scandinavia.

Papaveraceae

Papaver labradoricum (Fedde) Solstad & Elven, comb. et stat. nov. Basionym: *Papaver nudicaule* L. subsp. *radicatum* var. (gamma) *labradoricum* Fedde in Engl., Pflanzenreich IV-104(40):377. 1909. Type: GREENLAND: "Flora Groenlandiae boreali–occidentalis, Gebiet des Umanakfjords (70–71° N. Br.)," 9 Aug 1893, *E. Vanhöffen 35(94)* (Lectotype: B 10 0267999!). *Papaver radicatum* Rottb. subsp. *labradoricum* (Fedde) Fedde in Engl. & Prantl, Nat. Pflanzenfam., ed. 2, 17b:120. 1936. *Papaver lapponicum* (Tolm.) Nordh. subsp. *labradoricum* (Fedde) Knaben, Blyttia 16:78. 1958.

The eastern Canadian and Greenlandic *Papaver labradoricum* resembles *P. lapponicum* (Tolm.) Nordh. and *P. radicatum* Rottb. and has been considered as a subspecies of either one of these (e.g., Fedde 1936; Knaben 1958, 1959a, 1959b). The assignment to *P. radicatum* has been justified by morphology (Kiger & Murray 1997), that to *P. lapponicum* by sharing the same octoploid chromosome number ($2n = 56$), whereas *P. radicatum* is decaploid. In an unpublished study by Solstad et al., based on Structure analysis of AFLP DNA markers, *P. labradoricum* is a distinct entity (species) which joins comparatively closely with a Beringian species (*P.* cf. *detritophilum*) but is distant from the Atlantic European *P. radicatum* and the amphi-Atlantic *P. lapponicum*. Several morphological features are also shared with the Beringian species, but *P. detritophilum* is hexaploid ($2n = 42$) . A separation is further supported by the low fertility found by Knaben (1959b) in crosses between *P. labradoricum* on one hand and *P. lapponicum* and *P. radicatum* on the other, at the level of crosses between species according to Knaben. *Papaver labradoricum* is probably an allopolyploid with a complicated parentage, as are *P. lapponicum* and *P. radicatum*.

Brassicaceae

Arabidopsis petraea (L.) V.I. Doron. subsp. **septentrionalis** (N. Busch) Elven & D.F. Murray, comb. nov. Basionym: *Arabis septentrionalis* N. Busch, Bot. Mater. Gerb. Glavn. Bot. Sada RSFSR 3(3–4):10. 1922. Type: RUSSIA: northeastern European Russia (Novaya Zemlya) and northern Siberia (holotype?: LE). *Arabis petraea* (L.) Lam. subsp. *septentrionalis* (N. Busch) Tolm. in Tolm. & Blumenthal, Trudy Bot. Muz. 23:204. 1931. *Cardaminopsis septentrionalis* (N. Busch) O.E. Schulz in Engl. & Prantl, Nat. Pflanzenfam., ed. 2, 17b:541. 1936.

O'Kane and Al-Shehbaz (1997) proposed *Arabidopsis petraea* s. lat. as one of three subspecies of *Arabidopsis lyrata* (L.) O'Kane & Al-Shehbaz. Tolmachev (1975) considered the arctic Russian material as two subspecies of *Arabis petraea* (L.) Lam. Doronkin in Malyschev and Peschkova (1994) accepted only a collective *Cardaminopsis petraea* (L.) Hiitonen. We have studied herbarium material of the three proposed entities (*"petraea,"* *"septentrionalis,"* and *"umbrosa"*) and have also seen all three in the field in northern Europe, Siberia, and Alaska–Yukon. They are allopatric to slightly parapatric, with *"umbrosa"* in northwestern North America and northern–northeastern Asia (slightly overlapping with the next), *"septentrionalis"* in northern Asia and northeastern Europe, and *"petraea"* in northwestern and central Europe. There are other, non-arctic entities in the group. We are able to recognize the arctic entities on morphological criteria, and transitional forms have not been documented. *Arabidopsis petraea* s. lat. also differs in some morphological characters from *A. lyrata–kamtschatica*, without documented intermediates. The choice is between treating the arctic taxa as

three species or as three subspecies of *A. petraea*. Pending a combined molecular and morphological investigation of the entire aggregate applying molecular markers more suitable to specific/subspecific variation in recently evolved taxa, we propose to treat them as three subspecies.

Arabidopsis petraea (L.) V.I. Dorof. subsp. **umbrosa** (Turcz. ex Steud.) Elven & D.F. Murray, comb. nov. Basionym: *Arabis umbrosa* Turcz. ex Steud., Nomencl. Bot. 2:118. 1824. Type: RUSSIA: Siberia: "in sabulosis ad fl. Irkut," *Turczaninow* (holotype: MW). *Arabis petraea* (L.) Lam. subsp. *umbrosa* (Turcz. ex Steud.) Tolm., Fl. Arct. URSS 7:97. 1975. *Cardaminopsis petraea* (L.) Hiitonen subsp. *umbrosa* (Turcz. ex Steud.) Peschkova, Fl. Tsentr. Sib. 1:396. 1979.

Arabis arenicola (Richardson ex Hook.) Gelert var. *pubescens* (S.Watson) Gelert, Bot. Tidsskr. 21:290. 1898. Type: CANADA: Hudson Bay, York Factory.

Arabis media N. Busch, Bot. Mater. Gerb. Glavn. Bot. Sada RSFSR 3(3–4):11. 1922. Type: RUSSIA: eastern Siberia (LE). *Cardaminopsis media* (N. Busch) O.E. Schulz in Engl. & Prantl, Nat. Pflanzenfam., ed. 2, 17b:541. 1936.

The two entities subsp. *septentrionalis* and subsp. *umbrosa* are morphologically close but, as far as we have observed (herbarium, field in northern Sakha), they are without intermediates in the area of sympatry in northern Siberia.

Saxifragaceae

The phylogenetic analyses of Soltis et al. (1996, 2001) show that there are two major branches of genera in Saxifragaceae, and that a large segregate of traditional *Saxifraga* L., i.e., *Micranthes* Haw. (s. lat.) together with, e.g., *Chrysosplenium* L., belongs in a different branch from *Saxifraga* s. str. The molecular evidence makes it difficult to retain *Micranthes* within *Saxifraga*, and (like Brouillet & Gornall 2007) we accept it as a separate genus for the Checklist. Several combinations within *Micranthes* have been made in earlier times, and Brouillet and Gornall (2007) made the combinations they needed for their treatment for *Flora of North America*. This treatment does not cover the Asian taxa, and also for a few North American taxa we prefer another rank than chosen by Brouillet and Gornall.

Micranthes hieraciifolia (Waldst. & Kit. ex Willd.) Haw. subsp. **longifolia** (Engl. & Irmsch.) Elven & D.F. Murray, comb. nov. Basionym: *Saxifraga hieraciifolia* Waldst. & Kit. ex Willd. f. *longifolia* Engl. & Irmsch. in Engl., Pflanzenreich IV-117(67):24. 1916. Type: RUSSIA: Russian Far East: Chukchi Peninsula, St. Lawrence Bay, "St. Lorenzbusen," *Chamisso* (B), "Lütke's Hafen," *A. & A. Krause 163* (B), syntypes; *Saxifraga hieraciifolia* Waldst. & Kit. ex Willd. subsp. *longifolia* (Engl. & Irmsch.) Jurtz. & V.V. Petrovsky, Byull. Moskovsk. Obshch. Isp. Prir., Otd. Biol. 85, 6:101. 1980.

Saxifraga hieraciifolia Waldst. & Kit. ex Willd. subsp. *czukczorum* Chrtek & Soják, Preslia 53:71. 1981. Type: RUSSIA: Russian Far East, "Prov. Magadan, regio Tschukotsky, trajectus jugi Iskatenj, vicin. 32 km ...," 2 Aug 1967. *T. Derviz-Sokolova & T. Voronova* (holotype: PR).

Micranthes hieraciifolia is a polyploid to highly polyploid ($2n$ = 56–120), circumpolar-alpine species where Zhmylev in Elven et al. (2007) stated that: "This species shows considerable eco-morphological plasticity, not correlated with the chromosome numbers". We do not agree. Large parts of the material from northeastern Asia and Alaska, i.e., Beringia, deviate from the non-Beringian material in several features. We have surveyed northwestern North American and some northeastern Asian material (ALA, O) and find that the characters reported for subsp. *longifolia* vs subsp. *hieraciifolia* mostly hold, e.g.: leaves narrow, long-petiolate and acute with little pubescence vs broader, more short-petiolate and subacute to subobtuse and more hairy; stems with little pubescence vs distinctly pubescent; petals purple and as long as sepals vs pink and much shorter and narrower than sepals; and sepals purple vs green with purple dots. The inflorescence of ssp. *longifolia* is also more interrupted when fully grown, but there is overlap in this character. These characters largely separate between two easily identifiable groups: subsp. *longifolia* as narrowly amphi-Beringian and subsp. *hieraciifolia* as circumpolar and also common and co-occurring with subsp. *longifolia* in the amphi-Beringian regions. Subsp. *longifolia* is thereby fully sympatric with subsp. *hieraciifolia*, at least in an arctic context. There is also a suggested ploidal difference. All reports of comparatively low chromosome numbers ($2n$ = 56 and 63) are from northeastern Yakutia and Chukotka where these numbers are reported together with the prevalent much higher numbers everywhere else in northern and arctic regions ($2n$ = 100–120). From Alaska, only highly polyploidal counts are reported ($2n$ = >100 and 112), but these reports are partly from localities outside the range of subsp. *longifolia* as we have recorded it.

The names subsp. *longifolia* and subsp. *czukczorum* were published one year apart (1980 and 1981), and we assume that they represent the same taxon and that the authors were unaware of the other publication.

On the American side, subsp. *longifolia* is common in western Alaska north and east to the western Brooks Range (on the north coast as very rare east to Demarcation Point) and to the Kobuk and Yukon river valleys. In southwestern and south–central Alaska it is the exclusive race, e.g., in the Goodnews Bay area, Alaska Peninsula, and on Kodiak and smaller offlying islands.

Micranthes lyallii (Engl.) Small subsp. **hultenii** (Calder & Savile) Elven & D.F. Murray, comb. nov. Basionym: *Saxifraga lyallii* Engl. var. *hultenii* Calder & Savile, Canad. J. Bot. 38:418. 1960. Type: CANADA: British Columbia: Queen Charlotte Islands, Moresby Island, 20 mi S of Moresby Camp, 29 Jul–2 Aug 1957, *Calder, Savile & Taylor 23106* (holotype: DAO). *Saxifraga lyallii* Engl. subsp. *hultenii* (Calder & Savile) Calder & R.L. Taylor, Canad. J. Bot. 43:1393. 1965.

Brouillet and Gornall (2007) did not include the proposed northern race of *Saxifraga lyallii* in their recombinations. There is a gap in the range between the populations in the eastern Cordilleras (subsp. *lyallii*) and those in the western and northern Cordilleras (subsp. *hultenii*). We follow Calder and Savile (1960) and Calder and Taylor (1965) in acceptance of two major geographical races, i.e., subspecies in the Checklist concept.

Micranthes merkii (Fisch. ex Sternb.) Elven & D.F. Murray, comb. nov. Basionym: *Saxifraga merkii* Fisch. ex Sternb., Revis. Saxifrag., Suppl. 1:1. 1822. Type: RUSSIA: the Transbaikal area, "In humidis montis Jablonoi Chrebet," *Redowsky* (holotype?: LE).

Micranthes merkii is a distinct Asian species, assigned by Zhmylev in Elven et al. (2007) to its own sect. *Merkianae*.

Micranthes nelsoniana (D. Don) Small subsp. **aestivalis** (Fisch. & C.A. Mey.) Elven & D.F. Murray, comb. nov. Basionym: *Saxifraga aestivalis* Fisch. & C.A. Mey., Index Sem. Hort. Petrop. 1:37. 1835. Type: RUSSIA: S Siberia, Altai, 1817. Herb. *Fischer* (lectotype: LE), see Siplivinsky (1976). *Micranthes aestivalis* (Fisch. & C.A. Mey.) Small, N. Amer. Fl. 22, 2:145. 1905. *Saxifraga nelsoniana* (D. Don) Small subsp. *aestivalis* (Fisch. & C.A. Mey.) D.A. Webb, Feddes Repert. 69:154. 1964. *Micranthes nelsoniana* (D. Don) Small var. *aestivalis* (Fisch. & C.A. Mey.) Gornall & H. Ohba in Brouillet & Gornall, J. Bot. Res. Inst. Texas 1:1020. 2007.

Brouillet and Gornall (2007) recombined *Micranthes nelsoniana* var. *aestivalis*. This Asian plant is considered by some Russian authors as a separate species (i.e., Rebristaya 1984), by others as a major geographical race, i.e., a subspecies (Malyschev 1997; Zhmylev in Elven et al. 2007) due to occurrence of intermediate plants in the zone of overlap. We accept the latter proposal and make the necessary combination.

Micranthes nelsoniana (D. Don) Small. subsp. **insularis** (Hultén) Elven & D.F. Murray, comb. nov. Basionym: *Saxifraga punctata* L. subsp. *insularis* Hultén, Svensk Bot. Tidskr. 30:524. 1936. Type: ALASKA: Aleutian Islands, Carlisle Island, 15 Jul 1932, *E. Hultén 6591* (holotype: S); *Saxifraga nelsoniana* D. Don subsp. *insularis* (Hultén) Hultén, Bot. Not. 126:494. 1973. *Saxifraga insularis* (Hultén) Sipliv., Novosti Sist. Vyssh. Rast. 13:139. 1976. *Micranthes nelsoniana* (D. Don) Small. var. *insularis* (Hultén) Gornall & H. Ohba in Brouillet & Gornall, J. Bot. Res. Inst. Texas 1:1020. 2007.

Brouillet and Gornall (2007) recombined Hultén's *Saxifraga punctata* subsp. *insularis* (and Siplivinsky's *Saxifraga insularis*) as *Micranthes nelsoniana* var. *insularis*. This is an amphi-Pacific plant in very oceanic regions from Sakhalin, the Kuriles, Kamtchatka, and the Aleutian Islands to the very tip of the Alaska Peninsula, mostly well outside the range of *M. nelsoniana* s. str. (see Hultén 1968). Hultén (1968) reported intermediates towards subsp. *nelsoniana* in the zone of overlap on the Alaska Peninsula, Kodiak Island, and the Seward Peninsula. In our opinion, this is a case of subspecific variation, and we recombine accordingly.

Micranthes porsildiana (Calder & Savile) Elven & D.F. Murray, comb. nov. Basionym: *Saxifraga punctata* L. subsp. *porsildiana* Calder & Savile, Canad. J. Bot. 38:429. 1960. Type: CANADA: British Columbia, Murray Range at Azouzetta Lake, Hart Hwy, 4 Aug 1954. *Calder, Savile & Ferguson 14079* (holotype: DAO). *Saxifraga nelsoniana* D. Don subsp. *porsildiana* (Calder & Savile) Hultén, Bot. Not. 126:494. 1973. *Saxifraga porsildiana* (Calder & Savile) Jurtz. & V.V. Petrovsky, Bot. Zhurn. (Moscow & Leningrad) 58:1339. 1973.

Micranthes porsildiana was treated by Hultén (1968) as a subspecies of *Saxifraga punctata* auct. (= *Saxifraga (Micranthes) nelsoniana*), as was subsp. *insularis*. Brouillet and Gornall (2007) did not include or mention this entity. *Micranthes porsildiana* has a large overlap in range with *M. nelsoniana* in Alaska and eastern Chukotka.

Within these regions, we have several times in Alaska and Chukotka observed the two growing in close proximity, sometimes nearly mixed in the stands, without any evidence of intermediates. Zhmylev (1995) assigned *M. nelsoniana* and *M. porsildiana* (as *Saxifragas*) to different series, respectively, series *Aestivalis* Zhmylev and series *Reniformes* Zhmylev. Rank as two different species is merited.

Micranthes redofskyi (Adams) Elven & D.F. Murray, comb. nov. Basionym: *Saxifraga redofskyi* Adams, Nouv. Mém. Soc. Imp. Naturalistes Moscou 3:241. 1834. Type: RUSSIA: N Yakutia, "Fl. Lenam," *Adams ex herb. Trinius 2911* (lectotype?: MW).

Micranthes redofskyi is a diploid (2*n* = 20) belonging in sect. *Micranthes* together with at least three assumed close relatives: the seed-reproducing, amphi-Atlantic *M. stellaris* (L.) Galasso, Banfi & Soldano (2*n* = 28), the also seed-reproducing, Pacific North American *M. ferruginea* (Graham) Brouillet & Gornall (2*n* = 20), and the bulbil-reproducing, arctic circumpolar *M. foliolosa* (R.Br.) Gornall 2*n* = 40–64). All four species are morphologically distinct, but *M. foliolosa* has been assumed (Zhmylev in Elven et al. 2007) to be: "... a complex of 2–3 entities formed as a result of polyploidy of pseudoviviparous races of *Saxifraga stellaris*, *S. redofskyi* and *S. ferruginea*". The pseudovivipary (bulbils) could be the result of the polyploidization, and not a feature inherited from the parental entities. Arctic plants of *Micranthes foliolosa* are morphologically much closer to *M. redofskyi* than to *M. stellaris* or *M. ferruginea*. An unpublished investigation based on AFLP DNA markers and comparing these species (A. Tribsch, Salzburg) connects *M. foliolosa* sampled throughout the Arctic closely to *M. redofskyi* (and not to *M. stellaris*). The more floriferous populations of *M. foliolosa* are found in the Beringian regions, with lower chromosome numbers than the majority of the plants, overlapping in range with *M. redofskyi* and close to the range of *M. ferruginea*. *Micranthes redofskyi* is restricted to northeastern Asia from northern Yakutia eastwards to Chukotka.

Rosaceae

Dryas punctata Juz. subsp. **hookeriana** (Juz.) Jurtz., comb. nov. Basionym: *Dryas hookeriana* Juz., Izv. Glavn. Bot. Sada SSSR 28:325. 1929. Type: NORTH AMERICA (western): "Rocky Mountains," *Hooker* (LE, ex Herb. Fischer, Ledebour). *Dryas octopetala* L. subsp. *hookeriana* (Juz.) Hultén, Acta Univ. Lund., n.s., sect. 2, 42(1):1046. 1946.

Dryas hookeriana is recombined as a Cordilleran subspecies of the Asian and Beringian *D. punctata*. They share the adaxial leaf surface punctate glands, the abaxial leaf surface red, stipitate glands, and the absence of feathery hairs of the *D. octopetala* type.

Potentilla anserina L. subsp. **yukonensis** (Hultén) Soják ex Elven & D.F. Murray, comb. nov. Basionym: *Potentilla yukonensis* Hultén, Acta Univ. Lund., n.s., sect. 2, 42(1):1033. 1946. Type: U.S.A. Alaska: Palisades, 14 Jul 1902, *Hollick* (holotype: NY). Type of *Argentina subarctica* Rydb., N. Amer. Fl. 22(4):354. 1908. *Potentilla egedii* Wormsk. subsp. *yukonensis* (Hultén) Hultén, Ark. Bot. ser. 2, 7(1):72. 1968.

Potentilla anserina subsp. *yukonensis* is an interior northwestern North American regional race, differing from the other races (subsp. *anserina*, *egedii*, *pacifica*) to the same degree as these do among themselves. Treatment at the same rank is appropriate, either as four species or as four subspecies. We have chosen the latter course due to the frequent occurrence of intermediates in zones of contact. The name *Potentilla yukonensis* is a nomen novum as the epithet "*subarctica*" is inapplicable at species level due to *Potentilla subarctica* Rydb., N. Amer. Fl. 22(4):347. 1908. The combination *P. anserina* subsp. *yukonensis* has already been used as a nom. nud. in a key by Soják to section *Pentaphylloides* (Soják 1994:70).

Fabaceae

Hedysarum boreale Nutt. subsp. **dasycarpum** (Turcz.) D.F. Murray & Elven, comb. et stat. nov. Basionym: *Hedysarum dasycarpum* Turcz., Bull. Soc. Imp. Naturalistes Moscou 13:63. 1840. Type: RUSSIA: Sakha (Yakutia).

We consider the northwestern North American *Hedysarum mackenzii* and the northeastern Asian *H. dasycarpum* as allopatric subspecies of a more widely circumscribed *H. boreale*. The former is already combined as *H. boreale* Nutt. subsp. *mackenzii* (Richardson) S.L. Welsh.

Ericaceae

Rhododendron tomentosum (Stokes) Harmaja subsp. **decumbens** Elven & D.F. Murray, comb. nov. Basionym: *Ledum palustre* L. var. *decumbens* Aiton, Hort. Kew. 2:65. 1789. Type: CANADA: Hudson Bay (holotype:?). *Ledum decumbens* (Aiton)

Lodd. ex Steud., Nomencl. Bot., ed. 2, 2:20. 1841. *Ledum palustre* L. subsp. *decumbens* (Aiton) Hultén, Fl. Kamtchatka 4:8. 1930. *Rhododendron subarcticum* Harmaja, Ann. Bot. Fenn. 27:203. 1990. Nom. nov. for *Ledum decumbens* within *Rhododendron*. *Rhododendron tomentosum* (Stokes) Harmaja subsp. *subarcticum* (Harmaja) G.D. Wallace, Madroño 39:77. 1992. Nom. illeg.

Harmaja (1990) considered this entity a species and coined the name *Rhododendron subarcticum*, with *Ledum palustre* var. *decumbens* as its typonym, because a combination as *Rhododendron decumbens* would be a homonym (due to *Rhododendron decumbens* D.Don ex G.Don, Gen. Hist. 3:846. 1834). Wallace (1992) considered it a subspecies, as we do, and recombined it as subsp. *subarcticum*, probably unaware that the epithet *decumbens*, even if not available for a species, is available and has priority for a subspecies. We accordingly make a recombination on the priority name.

Vaccinium uliginosum L. subsp. **vulcanorum** (Kom.) Alsos & Elven, comb. et stat. nov. Basionym: *Vaccinium vulcanorum* Kom., Repert. Spec. Nov. Regni Veg. 13:236. 1914. Type: RUSSIA (Far East): Kamtchatka, "in alpibus peninsulae Kamtschatka circa lacus Kunotzkoje," 19 Aug 1909 and 02 Sep 1909, *V.L. Komarov* (LE). *Vaccinium uliginosum* L. subsp. *microphyllum* (Lange) Tolm. var. *vulcanorum* (Kom.) Jurtz., Byull. Moskovsk. Obshch. Isp. Prir., Otd. Biol. 85(6):105. 1980.

Vaccinium uliginosum L. is polymorphic as described by Young (1970). Komarov's *Vaccinium vulcanorum* is, according to Tolmachev and Yurtsev (1980), a prostrate-pulvinate dwarf shrub with small, imbricate, rotundate leaves persisting in winter, and globose berries. In a phylogenetic analysis by Alsos et al. (2005), the "*vulcanorum*" entity is a central node from which both an amphi-Pacific and a circumpolar clade emerge. Both phylogenetic and morphological evidence support the taxon *vulcanorum* as a race, preferrably as a subspecies.

Gentianaceae

Gentianopsis barbata (Froel.) Ma subsp. **raupii** (A.E. Porsild) Elven, comb. nov. Basionym: *Gentiana raupii* A.E. Porsild, Sargentia 4:60. 1943. Type: CANADA: Northwest Territory, Mackenzie District, Mackenzie River between Wrigley and Blackwater R, *A.E. Porsild 6571* (holotype: CAN). *Gentianopsis detonsa* (Rottb.) Ma subsp. *raupii* (A.E. Porsild) Á. Löve & D. Löve, Bot. Not. 128:517. 1976. *Gentianopsis raupii* (A.E. Porsild) Iltis, Sida 2:134. 1965. *Gentianella detonsa* (Rottb.) G. Don subsp. *raupii* (A.E. Porsild) J.M. Gillett, Ann. Missouri Bot. Gard. 44:217. 1957.

The entities of the *Gentianopsis detonsa–barbata* group in northern North America are still insufficiently studied, in spite of two revisions (Gillett 1957; Iltis 1965). They are rare taxa, restricted in their ranges and often disjunct. The "*raupii*" entity has been considered a separate species or a subspecies of *Gentianella* / *Gentianopsis detonsa*. Hultén (1968b) accepted *Gentiana raupii* as a separate species in northwestern Canada but said that it is "similar to *G. barbata*, but with fewer stem leaves; calyx rounded at base; corolla tube broadly obconic, the lobes broad, rounded". We support that view and hereby assign "*raupii*" to *Gentianopsis barbara* as a regional race. It occurs mainly along the Mackenzie River, and the entire range is within the glaciated areas. This is an entity that at some time (most probably postglacially) was able to differentiate in isolation from the main body of *Gentianopsis barbata*.

Asteraceae

Achillea alpina L. subsp. **multiflora** (Hook.) D.F. Murray & Elven, comb. et stat. nov. Basionym: *Achillea multiflora* Hook., Fl. Bor.-Amer. 1:318. 1833. Type: CANADA: "Throughout the woody country, and as far North as Fort Franklin," (holotype: ?). *Ptarmica multiflora* (Hook.) Tzvelev in Jurtz., Fl. Arct. URSS 10:107. 1987.

The North American representative of the *Achillea alpina* complex has been treated in most northwestern North American works (e.g., Hultén 1968a; Cody 1996, 2000) as *A. sibirica* Ledeb. Both names, *alpina* and *sibirica*, are based on Asian plants. Trock (2006) applied the name *A. alpina* without discussion for the North American plant. Russian authors have mostly treated the entities of the *A. alpina* complex as several species. Rank as largely allopatric subspecies of *Achillea alpina* is the better solution. The northwestern North American plants differ from the northeastern Asian ones in some quantitative features: capitulae more numerous, ligules smaller, and leaves slightly more dissected. We hereby recombine *A. multiflora* as a subspecies of *A. alpina*.

The *Achillea alpina* complex has been considered part of the segregate genus *Ptarmica* (e.g., Yurtsev

1987). Acceptance of *Ptarmica* as a separate genus is untenable according to phylogenetic evidence (Guo et al. 2004).

Artemisia kruhsiana Besser subsp. **alaskana** (Rydb.) D.F. Murray & Elven, comb. et stat. nov. Basionym: *Artemisia alaskana* Rydb., N. Amer. Fl. 34(3):281. 1916. Type: U.S.A.: ALASKA: Yukon River, Nulato–Nowikakat, 23–27 Jul 1889, *I.C. Russell* (holotype: US-417571).

Hultén (1968b) compared the northwestern North American *Artemisia alaskana* with the northeastern Asian *A. kruhsiana* and considered them related but specifically distinct. *Artemisia kruhsiana* was described with three allopatric to parapatric subspecies in northeastern Asia (Korobkov 1987). Korobkov (pers. comm.) indicated that *A. alaskana* was morphologically closest to *A. kruhsiana* subsp. *multisecta* (Leonova) Korobkov. We consider *A. alaskana* to be close enough to *A. kruhsiana* to be best considered a subspecies of the latter (see also Tkach et al. 2008 wherein *A. kruhsiana* and *A. alaskana* were very close in the phylogeny). In our opinion, the closest relationship is found with the Chukotkan subsp. *kruhsiana*. There is, however, an appreciable gap between the westernmost Alaskan occurrence of subsp. *alaskana* and the easternmost Asian occurrence of subsp. *kruhsiana*, as the species is absent from all of Chukchi Peninsula. We therefore propose subsp. *alaskana* as a fourth subspecies of *A. kruhsiana*.

Packera hyperborealis (Greenm.) Á. Löve & D. Löve subsp. **wrangelica** (Jurtz., Korobkov & V.V. Petrovsky) Jurtz., Korobkov & V.V. Petrovsky, comb. nov. Basionym: *Senecio hyperborealis* Greenm. subsp. *wrangelica* Jurtz., Korobkov & V.V. Petrovsky in Jurtz., Fl. Arct. URSS 10:216. 1987. Type: RUSSIA: Russian Far East, Wrangel Island, "pars centralis, in cursu superiore fl. Neizvestnaja (Incognita)," 22 Jul 1971, *V.V. Petrovsky & O.D. Schteinberg* (holotype: LE).

Transfer of *Senecio hyperborealis* to *Packera* necessitates the new combination. *Packera hyperborealis* s. str. is diploid (Packer 1972, northwestern Canada, $2n = 46$; Yurtsev & Zhukova 1972, northeastern Asia, $2n = 48$). Subspecies *wrangelica*, on the other hand, is hexaploid (Zhukova & Petrovsky 1987, Wrangel Island, $2n = 138$). This high number is more in accordance with the wide range of numbers found in the closely related *P. heterophylla* (Fisch.) E. Wiebe (= *Senecio cymbalaria* Pursh, *Senecio resedifolius* Less.).

Scorzoneroides autumnalis (L.) Moench subsp. **pratensis** (Hornem.) Elven, comb. nov. Basionym: *Apargia pratensis* Hornem., Hort. Bot. Hafn. 2:785. 1815. *Leontodon pratensis* (Hornem.) Rchb., Fl. Germ. Excurs. 1:253. 1831. *Leontodon autumnalis* L. var. *pratensis* (Hornem.) W.D.J. Koch, Syn. Fl. Germ. Helv. 418. 1837. *Leontodon autumnalis* L. subsp. *pratensis* (Hornem.) Gremli, Excursionsfl. Schweiz, ed. 3:242. 1878. *Scorzoneroides autumnalis* (L.) Moench var. *pratensis* (Hornem.) P.D. Sell, Fl. Great Brit. Irel. 4:531. 2006. *Leontodon autumnalis* L. var. *taraxaci* (L.) Hartm., Handb. Skand. Fl., ed. 4:252. 1843 (Basionym: *Hieracium taraxaci* L., Sp. Pl., ed. 2, 2:1125. 1763).

The new combination is necessitated by the transfer of *Leontodon autumnalis* L. to the genus *Scorzoneroides* Moench (cf., Sell & Murrell 2006). The provenience and characters of Hornemann's *Apargia pratensis* is not known to us, but the customary use of the name *pratensis* in northern Europe is for the plant considered here. The Nordic plants currently assigned under var./subsp. *pratensis* include Linnaeus' *Hieracium taraxaci* and are different from the central European alpine plants.

Solidago multiradiata Aiton subsp. **arctica** (DC.) Korobkov & Elven, comb. et stat. nov. Basionym: *Solidago virgaurea* L. var. (epsilon) *arctica* DC., Prodr. 5:339. 1836. Type: U.S.A: ALASKA: the Aleutian islands, "Unalaschka," and possibly RUSSIA: Russian Far East, Chukchi Peninsula: "ad sinum Sancti Laurentii." *Solidago multiradiata* Aiton var. *arctica* (DC.) Fernald, Rhodora 17:4. 1915. *Solidago compacta* Turcz., Bull. Soc. Imp. Naturalistes Moscou 13:73. 1840. Probably a nomen novum for var. *arctica* as a species.

Solidago multiradiata Aiton is widespread and polymorphic. The plants around the Bering and Chukchi seas in eastern Chukotka and western and southwestern Alaska constitute the westernmost extension of the range for *S. multiradiata* and differ in several quantitative features. Hultén (1968a) accepted a variety, var. *arctica*. Russian authors (e.g., Korobkov 1987) have instead treated it as a separate species, *S. compacta*. We prefer to see *S. compacta* or var. *arctica* as a regional race, i.e., a subspecies. It might be uniformly tetraploid ($2n = 36$), as indicated by Löve and Löve (1975), but both diploid and tetraploid counts are known from *S. multiradiata* s. str.

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HEUCHERA WOODSIAPHILA (SAXIFRAGACEAE), A NEW SPECIES FROM THE CAPITAN MOUNTAINS OF NEW MEXICO

Patrick J. Alexander

Biology Department, MSC 3AF
New Mexico State University
Las Cruces, New Mexico 88003, U.S.A.
paalexan@nmsu.edu

ABSTRACT

A new species in the Saxifragaceae, **Heuchera woodsiaphila** is described from the Capitan Mountains of Lincoln County, New Mexico. This species is similar to those of *Heuchera* section *Holochloa* subsection *Cylindricae* but is highly disjunct from described members of the subsection. *Heuchera woodsiaphila* is readily distinguished from other *Heuchera* in the area by its greenish-white to cream apetalous flowers with erect sepals 2.75–3.75 mm long. It is known from only small, scattered populations on forested granitic talus on the north and northeastern sides of Capitan Peak, between 2,550 and 2,900 m in elevation.

RESUMEN

Se describe una especie nueva, **Heuchera woodsiaphila** (Saxifragaceae) de las Capitán Mountains en Lincoln County, Nuevo México. Esta especie es similar a las de *Heuchera* sección *Holochola* subsección *Cylindricae*, pero geográficamente está muy alejada de miembros de la subsección descritos anteriormente. *Heuchera woodsiaphila* se distingue fácilmente de otras *Heuchera* en la región por sus flores apétalas de blanco-verdosas a ocroleucas con sépalos erectos de 2.75 a 3.75 mm de largo. Se conoce sólo de dos colectas en taludes graníticos de bosque en las laderas norte y noreste de Capitán Peak, en elevaciones de 2,550 a 2,900 m.

The Capitan Mountains are the most northeastern range in the greater Sacramento Mountains complex, a group of mountain ranges in Lincoln and Otero counties of south-central New Mexico which also includes Sierra Blanca, Carrizo Mountain, and the Sacramento Mountains proper. These mountain ranges include the highest point in the southern half of New Mexico, Sierra Blanca Peak at 3,649 m, and contain large areas over 2,500 m elevation. There are no similar mountain ranges nearby. The nearest peak exceeding 3,000 m is South Baldy in the Magdalena Mountains, ca. 190 km to the west-northwest, while the nearest peak equalling Sierra Blanca's height is Tesuque Peak in the Sangre de Christo Mountains ca. 320 km to the north. Consequently, there is a well-developed high-elevation flora in the Sacramento Mountains complex that is isolated from other areas with similar floras. This area contains some of the most southeastern populations of typical members of the Rocky Mountain flora, such as *Picea pungens* Engelm. and *Abies bifolia* A. Murr. and is home to 21 endemic plant taxa. Most botanical exploration in the area has been conducted in the Sacramento Mountains proper and on Sierra Blanca. The Capitan Mountains and Carrizo Mountain, both granite laccoliths on the northern end of the Sacramento Mountains complex, are comparatively difficult to access and distant from centers of botanical research. Their floras remain poorly known. It is thus no coincidence that the Capitan Mountains yielded the most recently described of the endemics of the Sacramento Mts. complex, *Astragalus kerrii* Knight & Cully (Knight & Cully 1991), as well as the presently described species.

The endemic flora of the Sacramento Mountains complex has traditionally included a *Heuchera*, *H. wootonii* Rydb. of section *Parvifoliae* (Small & Rydberg 1905; Calder & Savile 1959; Rosendahl et al. 1936). This species, however, has recently been reported elsewhere and its taxonomic circumscription is uncertain (New Mexico Rare Plant Technical Council 1999; B. Shipes, personal communication). With the presently-described *H. woodsiaphila*, the Sacramento Mountains complex gains an endemic *Heuchera* at the same time that it risks losing one.

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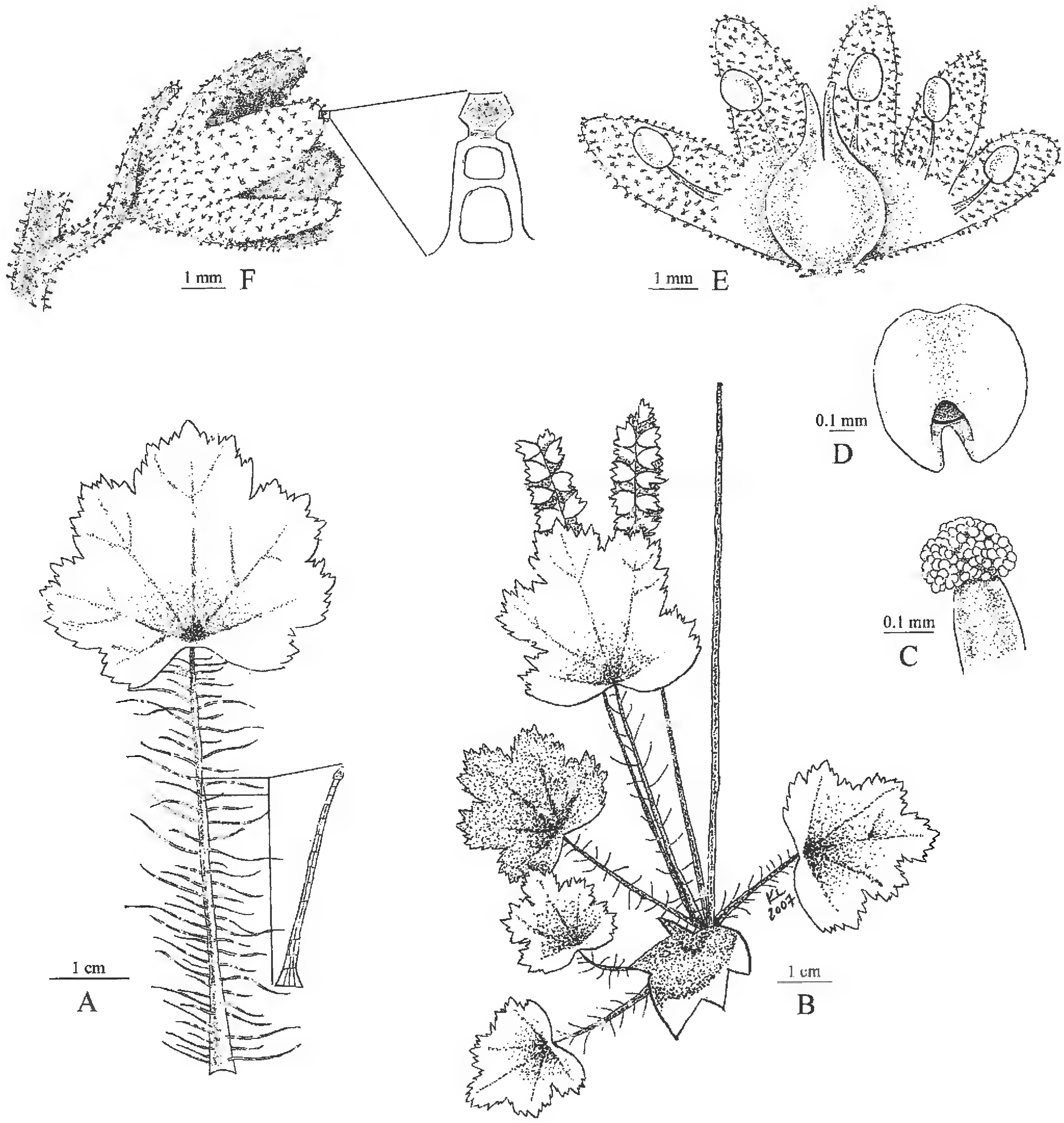

Fig. 1. ***Heuchera woodsiaphila*, based on *P.J. Alexander 390* and *S. Chaddie* 135. A. Basal leaf. B. Habit. C. Stigma. D. Anther. E. Dissected flower. F. Flower, side view.**

Heuchera woodsiaphila P.J. Alexander, sp. nov. (**Figs. 1–3**). Type: U.S.A. New Mexico. Lincoln Co.: NE side of Capitan Peak on the upper part of the Capitan Peak Trail, 33° 35' 37"N 105° 15' 31.5"W, elev. 9200 ft, steep NE slope, duff soil among granite boulders in stabilized, forested talus, 17 Jul 2006, *P.J. Alexander 390.* (holotype: NMC; isotypes: UNM, ARIZ, ALA, MO, DUKE).

Species novum characteribus *Heuchera* sect. *Holochloa* Nutt. subsect. *Cylindricae* Rydb., maxime similis a *Heuchera saxicola* E. Nels. (Idaho, Montana, Oregon) a qua differt foliis basibus cordatis, pubescentia viscido carenti, et bracteis superis brevioribus (a 5 mm). Differt a *Heuchera* cetera in New Mexico floribus petala carentibus ac sepala erectas viridi-albas vel cremeas.

Herbs, perennial, acaulescent from an elongate, branching caudex; **leaves** with *stipules* lanceolate, 5–8 mm long, adnate to the petioles ± 2/3 their length, entire, glandular-puberulent, ciliate distally with whitish, gland-tipped trichomes to 2 mm long; *petioles* of the larger leaves ascending, 4–8 cm long, glandular-puberulent and sparsely villous with white, minutely gland-tipped, multicellular hairs to 5(–8) mm long; *blades* green, sub-reniform to broadly ovate, the base cordate, the larger leaves 2.5–4 cm wide and 2–3.5 cm long, shallowly 5-lobed, with ± 25–30 broad teeth, these mucronate, the whitish mucros to 1 mm long,

Fig. 2. Habit (left) and flowers (right) of *Heuchera woodsiaphila* photographed by myself near the type locality on Capitan Peak. Additional photographs can be found at http://polyploid.net/Heuchera/.

minutely gland-tipped, secondary teeth often reduced to mucros on the lateral margins of the primary teeth, margins also with minute, translucent, gland-tipped projections, surfaces glandular-pulverulent, also sparingly villous on the veins adaxially, with white, gland-tipped hairs to 2 mm long; **flowering stems** 8–20 cm high, subscapose, glandular-puberulent throughout, usually with 1–3 sterile bracts (or these absent), the sterile bracts with green blades, resembling the basal leaves, 4–15 mm long by 4–15 mm wide, 3–5 lobed, lobes of the larger bracts crenate-dentate, the teeth acuminate to short-mucronate, surfaces glandular-pulverulent; **inflorescences** 3–4 cm long, secund or subsecund, flowers born in small cymules of 1–4 flowers, peduncles mostly ± 1 mm, the lower often elongate to 7 mm, the pedicels 1–2 mm; bracts of the inflorescence variable, the lowest resembling the leaf-like sterile bracts, the rest linear, 3–5 mm long, pale green or whitish at anthesis, often becoming pinkish with age, glandular-puberulent, the stipules represented by lateral aristate teeth or absent, margins entire or distally fimbriate, bractlets of the cymules becoming progressively smaller; **flowers** apetalous, regular or nearly so, 5.25–6 mm long at anthesis, the hypanthium 1–1.5 mm long, widening gently from the inferior portion of the ovary; *sepals* 5, equal, greenish-white to cream at anthesis, the tips sometimes becoming pinkish in fruit, oblong with obtuse tips, 2.75–3.75 mm long, densely glandular-puberulent on both surfaces; *stamens* 5, arising from the hypanthium slightly below the bases of the sepals, ± 2 mm long, gently incurved, persisting until after dehiscence of the capsule, the filaments ± 1.5 mm long and the anthers ± 0.7 mm long, deeply cordate, orange, red or purplish at anthesis; *gynoecium* of 2 carpels, at anthesis with the inferior portion of the ovary hemispheric, 2–2.5 mm wide and ± 1.25 mm long, the styles and beaks of the carpels separate for ± 2 mm, the last 1–1.5 mm of this comprising the true closed styles, styles included with capitate stigmas slightly wider than the styles; **capsules** ovoid with a nearly hemispherical base, 5.5–6.5 mm long, the beaks of the carpels splitting longitudinally on their interior surfaces, the styles slightly curved outwards, equaling the sepals or exserted to 1 mm, the true closed styles 1–1.5 mm long above the beaks of the carpels; **seeds** dark brown, narrowly ellipsoid, ± 0.75 mm long by ± 0.3 mm wide, the surfaces echinulate.

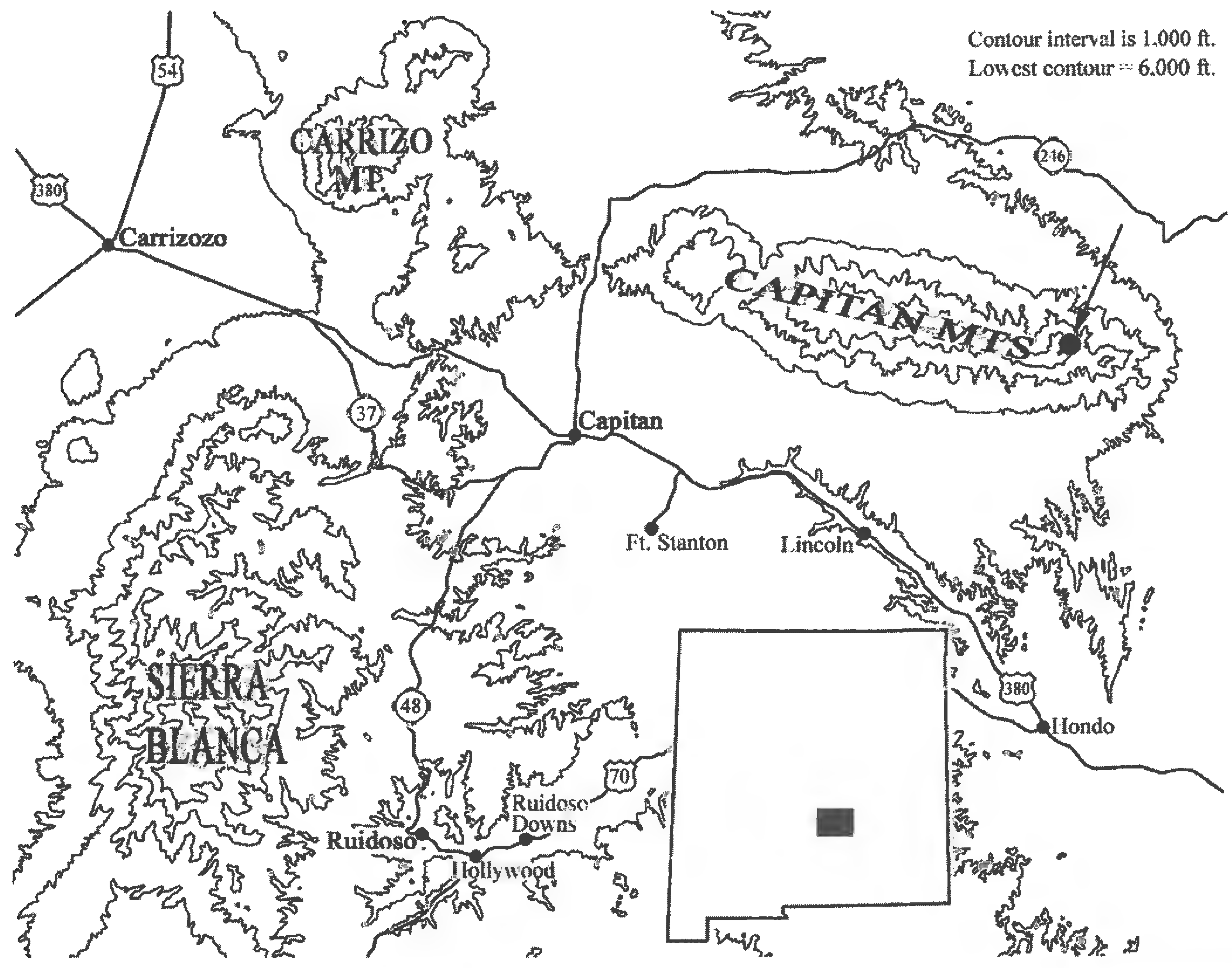

Fig. 3. Known distribution of *Heuchera woodsiaphila*. Map drawn based on the USGS 1:250,000 Roswell quadrangle topographic map.

Etymology.—The specific epithet refers to the close association of this species with *Woodsia plummerae* Lemmon, which is ubiquitous at populations of *H. woodsiaphila* and is often the most abundant vascular plant in the immediate vicinity.

Phenology.—Specimens collected in July and August include both mature fruits and flowers at anthesis.

Geography and habitat.—*Heuchera woodsiaphila* is presently known only from Capitan Peak at the eastern end of the Capitan Mountains in Lincoln County, New Mexico (Fig. 3), where it has been observed from 2,550 to 2,900 m in elevation along the Capitan Peak Trail, Lincoln National Forest Trail #64. It is found at locally moist sites on north or northeast, stable, forested granitic talus, usually under cover of *Pseudotsuga menziesii* (Mirb.) Franco or *Abies concolor* Lindl. & Gord. and in association with *Woodsia plummerae*. These moist sites are many, but small and scattered. Much of the forest in this area has burned recently, and *H. woodsiaphila* appears to be equally abundant in burned and unburned areas.

Distinction from other Heuchera. *Heuchera woodsiaphila* is very similar to members of *Heuchera* section *Holochloa* Nutt. subsection *Cylindricae* Rydb. Like other members of subsection *Cylindricae*, it has elongate (5–8 mm in the subsection), white or whitish, actinomorphic or slightly zygomorphic, apetalous flowers with campanulate hypanthia and long (2.5–6 mm in the subsection), erect sepals. *Heuchera woodsiaphila* is widely disjunct from other members of the subsection, which are present in the northwestern United States and adjacent Canada. The nearest known populations of *H. cylindrica* Dougl. are in northeastern Nevada more than 900 km to the northwest.

Taxonomy of subsection *Cylindricae* is uncertain. The subsection includes up to 9 taxa at varietal to specific ranks, all of these taxa apparently intergrading to a greater or lesser extent (Calder & Savile 1959;

Rosendahl et al. 1936). In comparatively recent floras of the northwestern United States and adjacent Canada, subsection *Cylindricae* is generally treated as two species: *H. chlorantha* Piper and a highly polymorphic *H. cylindrica* (e.g., Douglas et al. 1991; Hitchcock & Cronquist 1973). Based on the most recent monographic treatment of subsection *Cylindricae* (Calder & Savile 1959), *H. woodsiaphila* is most similar to *H. saxicola* E. Nelson and *H. cylindrica* Dougl. vars. *cylindrica* and *orbicularis* (Rosend. et al.) Calder & Savile. It differs from the former in lacking dense, viscid pubescence, in having leaves with cordate bases, and in having smaller bracts within the inflorescence. *Heuchera woodsiaphila* differs from the above-mentioned varieties of *H. cylindrica* in having shorter scapes (8–20 vs 22–70 cm) and usually having sterile bracts with well-developed blades. Although Calder and Savile (1959) do not discuss characters of the androecium or gynoecium in depth, these are described in detail by Rosendahl et al. (1936). Following the latter treatment, *H. woodsiaphila* also differs from the known members of subsection *Cylindricae* in having shorter anthers (0.7 vs. 0.9–1.5 mm) and longer true closed styles (1–1.5 vs. ≤ 0.5 mm). To aid in distinction of this species from others in New Mexico, a key is provided below.

KEY TO THE *HEUCHERA* SPECIES OF NEW MEXICO

1. Flowers pinkish to red.
   2. Stamens about equaling or slightly exceeding the hypanthium; petals much shorter than the sepals or absent ____ **H. sanguinea** Engelm.
   2. Stamens and petals both equaling or exceeding the sepals.
      3. Hypanthium 1 mm long or less at its shortest point; styles strongly-exserted, exceeding the sepals by at least 1 mm ____ **H. rubescens** Torr.
      3. Hypanthium 1.5 mm long or more at its shortest point; styles only slightly exserted, exceeding the sepals by less than 1 mm ____ **H. pulchella** Woot. & Standl.
1. Flowers white, cream, or greenish white.
   4. Hypanthia deep, campanulate; petals erect and shorter than to equaling the sepals, or absent; sepals whitish basally with greenish tips or whitish throughout, erect basally and spreading apically or erect throughout.
      5. Petals absent; sepals 2.5 mm or longer; scapes 8–20 cm ____ **H. woodsiaphila** P.J. Alexander
      5. Petals present; sepals 2 mm or less; scapes 25 cm or more.
         6. Sepals glandular-puberulent, the longest hairs ≤ 0.2 mm; true closed styles present, ≥ 0.5 mm long ____ **H. novomexicana** Wheelock
         6. Sepals glandular-hirsute, the longest hairs 0.3–0.6 mm long; true closed styles < 0.5 mm long or apparently absent ____ **H. glomerulata** Rosend. et al.
   4. Hypanthia shallow, saucer-shaped; petals spreading, usually longer than the sepals, rarely equaling them; sepals green throughout, spreading.
      7. Petioles hirsute; plants of Lincoln, Otero, and Catron Counties. ____ **H. wootonii** Rydb.
      7. Petioles merely puberulent; plants of north-central New Mexico ____ **H. parvifolia** Nutt. ex Torr. & A. Gray

Although production of new comprehensive keys for subsection *Cylindricae* best awaits revision of the group and is thus beyond the scope of the present work, the key of Calder and Savile (1959) can be modified to accommodate *H. woodsiaphila* by replacing the first half of couplet "2" with the following:

2. Well-developed bracts of panicle 4.0–15.0 mm long and 2.5–15.0 mm wide, excluding cilia, often green and leaflike; leaf blades conspicuously viscid or not
   2a. Leaf blades with many viscid hairs, especially above, retaining soil and plant particles; leaf bases truncate to broadly cuneate, rarely slightly cordate ____ **H. saxicola** E. Nelson
   2b. Leaf blades glandular-pulverulent but not viscid, not retaining soil and plant particles; leaf bases strongly cordate ____ **H. woodsiaphila** P.J. Alexander

PARATYPE. **U.S.A. NEW MEXICO: Lincoln Co.:** Capitan Peak, 13 Aug 1995, S. *Chaddie 135* (NMC).

Other specimens.—Of the other major regional herbaria only UNM and UTEP have specimens of *Heuchera* from the Sacramento Mountains complex. On viewing the collections of these herbaria no additional specimens of *H. woodsiaphila* were found.

Discussion.—Although a conspicuous component of the flora at Capitan Peak, *H. woodsiaphila* was still unknown when I stumbled upon it while hiking the peak in 2006. Although I quickly found S. Chaddie's

1995 specimen (also from Capitan Peak but misidentified as *H. novomexicana*) and determined it was the same as my new collection, I could not identify these plants. Discussion with other botanists in the state, notably Robert Sivinski, quickly made it clear that this was not a species known from New Mexico but left open the possibility that it was a species well-known elsewhere. In the comprehensive monograph of *Heuchera* by Rosendahl et al. (1936), *H. woodsiaphila* clearly falls into *Heuchera* section *Holochloa* subsection *Cylindricae*. Although *H. woodsiaphila* is readily distinct from taxa of subsection *Cylindricae* as they are described in the monographic treatments of Rosendahl et al. (1936) and Calder and Savile (1959), the confused nature of this subsection makes it difficult to ascertain the limits of the considerable variation found in both the named taxa and their various hybrids. The proper status of *H. woodsiaphila* is thus difficult to determine at present. Although it could be argued that *H. woodsiaphila* is better treated as a variety of *H. cylindrica*, hiding variation within species tends in practice to obscure it or give the impression that it is unimportant. Further, this would not in any way reduce the taxonomic uncertainty in subsection *Cylindricae*, but would merely maintain the same uncertainties at a different taxonomic level. Unfortunately an adequate resolution to this problem must await a modern revision of the subsection.

Although *H. woodsiaphila* is very similar morphologically to members of subsection *Cylindricae*, the possibility that this species may result from hybridization among known New Mexican *Heuchera* and be only convergent with members of subsection *Cylindricae* should not be excluded. Leaves of *H. woodsiaphila* are identical in appearance to those of some specimens of the polymorphic *H. rubescens*, a member of section *Rhodoheuchera* R. B. & L. subsection *Rubescentes* Rydb. and, although difficult to distinguish in technical characters, seem subjectively rather different from those of subsection *Cylindricae*. Furthermore, most characteristics in which this species differs from New Mexican members of section *Holochloa*, including the long sepals, short scapes, and well-developed, leaf-like sterile bracts of the scape, can be found in *H. rubescens*. Molecular phylogenetic analyses will probably be necessary to ascertain the affiliations of *H. woodsiaphila* with any certainty.

The highly restricted distribution of *H. woodsiaphila* is also noteworthy. The apparent limitation of this species to high-elevation, forested talus may explain this limited distribution. On the Capitan Peak Trail, *H. wootonii* occurs in similar habitat to *H. woodsiaphila* but at lower elevations (1,950 to 2,400 m). On trips to the otherwise geologically and floristically similar mountains nearby, Sierra Blanca and Carrizo Mountain, I could find neither high-elevation, forested talus nor *H. woodsiaphila*. Instead, on these mountains the talus is either bare or has only low, tangled vegetation and *H. wootonii* occurs to at least 3,000 m. In these mountains, *H. wootonii* is often found near *Woodsia neomexicana* Windham or *W. phillipsii* Windham. Here *W. plummerae*, which is typically present with *H. woodsiaphila*, is conspicuously absent. Both the Capitan Mountains and nearby Carrizo Mountain are poorly explored botanically, however, and *H. woodsiaphila* may well have a broader geographic or ecological distribution than is presently known.

ACKNOWLEDGMENTS

I thank Richard Spellenberg for assistance and motivation in preparing the manuscript, Katy Levings for creating the illustration, Guy Nesom for translating the diagnosis into Latin, Ana Lilia Reina-Guerrero for vetting the Spanish translation of the abstract, and Robert Sivinski for helpful discussion regarding the distinctness of *H. woodsiaphila*. Larry Mellichamp, Barbara Greene Shipes, Charles B. McDonald, and Jane Mygatt provided helpful review comments.

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BOOK NOTICE

Laurence M. Hardy (ed.). 2008. **Bulletin of the Museum of Life Sciences, No. 14: Freeman and Custis Red River Expedition of 1806: Two Hundred Years Later.** (pbk.). Museum of Life Sciences, Louisiana State University Shreveport, One University Place, Shreveport, Louisiana 71115-2399, U.S.A. (**Orders:** www.lsus.edu/lsusmus, lhardy@lsus.edu, 1-318-797-5338, 1- 318-797-5222 fax). 368 pp., 7" × 10".

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THREE NEW SPECIES OF *IXORA* (RUBIACEAE) FROM THE STATE OF TOCANTINS, BRAZIL

Piero G. Delprete

Federal University of Goiás, Campus II
Institute of Biological Sciences - ICB-1
Department of General Biology/Botany
74001-970 Goiânia, Goiás, BRAZIL
pdelprete@hotmail.com

ABSTRACT

During the preparation of the Rubiaceae treatment for the *Flora de Goiás e Tocantins*, three undescribed species of *Ixora* were found, all understory shrubs from the state of Tocantins (Brazil). **Ixora congestiflora** Delprete is known from two collections, one from the Parque Estadual do Cantão, just north of the Ilha do Bananal, and the other from the state of Maranhão, near the Tocantins River, in semideciduous and gallery forests with Amazonian influence. **Ixora araguaiensis** Delprete is also known from two collections from northern Tocantins, near the Araguaia River. **Ixora irwinii** Delprete is known by a few collections from the gallery forests of northern Tocantins. The three species are here described and illustrated. A key to the native species of Goiás and Tocantins is included.

Key words: *Ixora*, Ixoroideae, Rubiaceae, Tocantins, Brazil, Amazon Basin

RESUMO

Durante a preparação do tratado das Rubiaceae para a *Flora de Goiás e Tocantins*, foram encontradas três novas espécies de *Ixora*, sendo todas representadas por arbustos umbrófilos das florestas do Estado de Tocantins. **Ixora congestiflora** Delprete é conhecida por duas coletas, uma no Parque Estadual do Cantão, ao norte da Ilha do Bananal, e a outra no Estado de Maranhão, perto do Rio Tocantins, em florestas semidecíduas e de galeria com influência amazônica. **Ixora araguaiensis** Delprete é também descrita por duas coletas realizadas no norte do Estado de Tocantins, perto do Rio Araguaia. **Ixora irwinii** Delprete é conhecida por poucas coletas em florestas de galeria no norte do Estado de Tocantins. As três espécies são aqui descritas e ilustradas. Uma chave para as espécies nativas dos Estados de Goiás e Tocantins é incluída.

Palavras chave: *Ixora*, Ixoroideae, Rubiaceae, Tocantins, Brasil, Bacia Amazônica.

The state of Tocantins was separated from the state of Goiás in 1988, and since then the Brazilian government encouraged its economic development through the creation of new cities and new roads, and by stimulating immigration from other Brazilian states. For example, Palmas, the state capital and the newest city in Brazil, in 2007 has already grown to more that 200,000 inhabitants, and many other new urban agglomerations have been founded throughout the state during the last decade. As for the vegetation, the southern portion of the state is located within the Brazilian Savannah (Cerrado Biome). Whereas, the central-northern portion of the state is an area of transition between the Savannah and the Amazon Basin, with a floristic composition from both biomes and species unique to this vegetation. This is particularly true for the floristic composition of the gallery forests along water courses flowing northwards, which act as migratory routes connected with the Amazon Basin. This region continues to be botanically little-known, and only recently has received some attention through several botanical expeditions organized by local institutions. At the same time, the entire state is under rampant anthropic pressure due to aggressive and extensive farming, construction of new state roads leading to remote areas, and massive human migration that took place during the last two decades. In addition, even the potentially protected areas are not safe from this ongoing environmental destruction, as it is common to see large herds of cows grazing among the vegetation of the state and national parks present in this state.

During the preparation of the Rubiaceae treatment for the *Flora de Goiás e Tocantins*, three interesting species of *Ixora* were encountered. All of them are understory shrubs collected in the forests of the central-northern portion of the state of Tocantins. After consulting all the available literature dedicated to South

American *Ixora* (Müller Argoviensis 1875, 1881; Standley 1937; Steyermark 1967; Delprete 2003, 2007, submitted; Delprete & Cortés-B. 2007; Delprete et al. 2005; Taylor & Steyermark 2004), and comparison with the specimens present in herbaria with large Brazilian collections (see acknowledgments), it was concluded that they are, in fact, new to science. One species, *Ixora congestiflora* Delprete is known from two collections, one from the Parque Estadual do Cantão, just north of the Ilha do Bananal, and the other from the state of Maranhão, near the Tocantins River, in semideciduous and gallery forests with Amazonian influence. The second species, *Ixora araguaiensis* Delprete is also known from two collections from northern Tocantins, near the Araguaia River. The third species, *Ixora irwinii* Delprete, is known from a few collections from gallery forests in northern Tocantins. With these three new species, described and illustrated below, and a few unpublished synonymies (Delprete, submitted), the number of Neotropical species of *Ixora* is approximately 45, which is the same number earlier estimated by Delprete (2003).

1. Ixora congestiflora Delprete, sp. nov. (**Fig. 1**). TYPE: BRAZIL: TOCANTINS: Mun. Caseara, Parque Estadual do Cantão, transecto 11, floresta estacional semidecídua, 09°18'00"S, 50°01'57"W, 15 Jan 2000 (fl), *P.E. Nogueira & M. Richter 692* (HOLOTYPE: IBGE; ISOTYPE: NY).

Ab *Ixora bracteolari* Müll. Arg., quae similis inflorescentia compacta et pauciflora, differt bracteis subtendentibus nullis (nec bracteis subtendentibus foliaceis), alabastris in parte summa fusiformibus (nec ovoideis), et corollis 13–14.5 mm longis (nec 7.5–8 mm longis).

Shrub to 2 m tall; branchlets glabrous. **Stipules** basally connate, 3.5–8 × 3–4 mm, base ovate, 1.5–4 mm long, arista 2–4 mm long, glabrous outside, densely sericeous-pubescent and intermixed with colleters inside. **Leaves** opposite, petiolate; petioles 5–15 mm long, glabrous; blades obovate to oblanceolate, (3.5–)7.3–12.5 × (1.2–)3–4.5 cm, base acute or decurrent, apex obtuse to acute, or acuminate (acumen deltoid, 5–7 mm long), subcoriaceous, glabrous throughout; secondary veins 12–18 each side, subsecondary veins parallel, about the same number as the secondaries. **Inflorescences** terminal, subpedunculate, very compact, reduced-trichotomous, glabrous throughout, 21–30-florous; the three branchlets 1–2 mm long, ending with three 2–3(–4)-florous cymules; bracts subtending the cymules ovate-acuminate, 1.5–2 mm long; bracteoles 1 or 2 each flower, ovate, 0.5–0.7 mm long, glabrous. **Flower buds** with tube narrowly-cylindrical, and fusiform in upper part (lobed portion). **Flowers** sessile. **Hypanthium** obovoid, 0.5–0.7 mm long, glabrous. **Calyx** cupular; tube 0.5–1.4 mm long; lobes unequal, narrowly triangular, 0.5–1.2 mm long, glabrous. **Corolla** hypocrateriform, 13–14.5 mm long, red externally, cream-white internally; tube narrowly-cylindrical, 8–8.5 × 0.7–0.9 mm, glabrous throughout; lobes narrowly-lanceolate, 5–6.5 × 1.5–1.8 mm, apex acuminate. **Stamens** exserted, reflexed among the corolla lobes; anthers oblong, ca. 3 mm long. **Style** exserted just above the mouth, 9.5–10 mm long; style branches narrowly oblong, 0.7–1 mm long (not fully expanded). **Fruits** unknown.

Distribution and ecology.—Known only from two collections, as a shrub growing in semideciduous seasonal forest in the Parque Estadual do Cantão, near the Araguaia River, in the municipality of Caseara, and the other from the state of Maranhão, in gallery forest near the Tocantins River (on the other side of the state of Tocantins, and an area soon to be submerged because of the construction of a dam).

Taxonomic observations.—This species is similar to *Ixora bracteolaris* Müll. Arg. (Müller Argoviensis 1875, 1881; Delprete 2007), because of the fasciculate, pauciflorous inflorescence, but differs from it by the absence of subtending bracts (vs. subtending bracts foliose, oblong-elliptic, 5–12 × 2--3 mm in *I. bracteolaris*), floral buds fusiform in the upper part (vs. ovoid in the upper part), and corollas 13–14.5 mm long (vs. 7.5–8 mm long).

Additional specimens examined: **BRAZIL: MARANHÃO:** Mun. Estreito, left margin of Tocantins River, mouth of Rio Feio, 140 m, 06°44'15"S, 47°29'26""W, 14 Jan 2008 (fl), *G.P. Silva & G.A. Moreira 12598* (CEN, UFG).

2. Ixora araguaiensis Delprete, sp. nov. (**Fig. 2**). TYPE: BRAZIL: TOCANTINS: Mun. Pium, Ilha do Bananal, Parque Nacional do Araguaia, Posto de fiscalização do Projeto Quelônios da Amazônia, 09°50'57"S, 50°11'31"W, 190 m, 26 Mar 1999 (fl), *M.A. da Silva, R.C. Mendonça, E. Cardoso, A.D. dos Santos, N.G. Sousa, N.R. Oliveira & J.T. dos Santos 4164* (HOLOTYPE: IBGE; ISOTYPE: NY).

Frutex 1 m alta *Ixorae brevifoliae* Benth. similis inflorescentiis terminalibus corymbosis vel paniculatis, sed differt statura minore (nec statura arboris ad 20 m altae), inflorescentis 12–18-floris (nec 45–150-floris), tubo corollae medium versus contracto (nec tubo corollae cylindrico), venis secundariis foliorum utrinque 10–15 (nec 15–40).

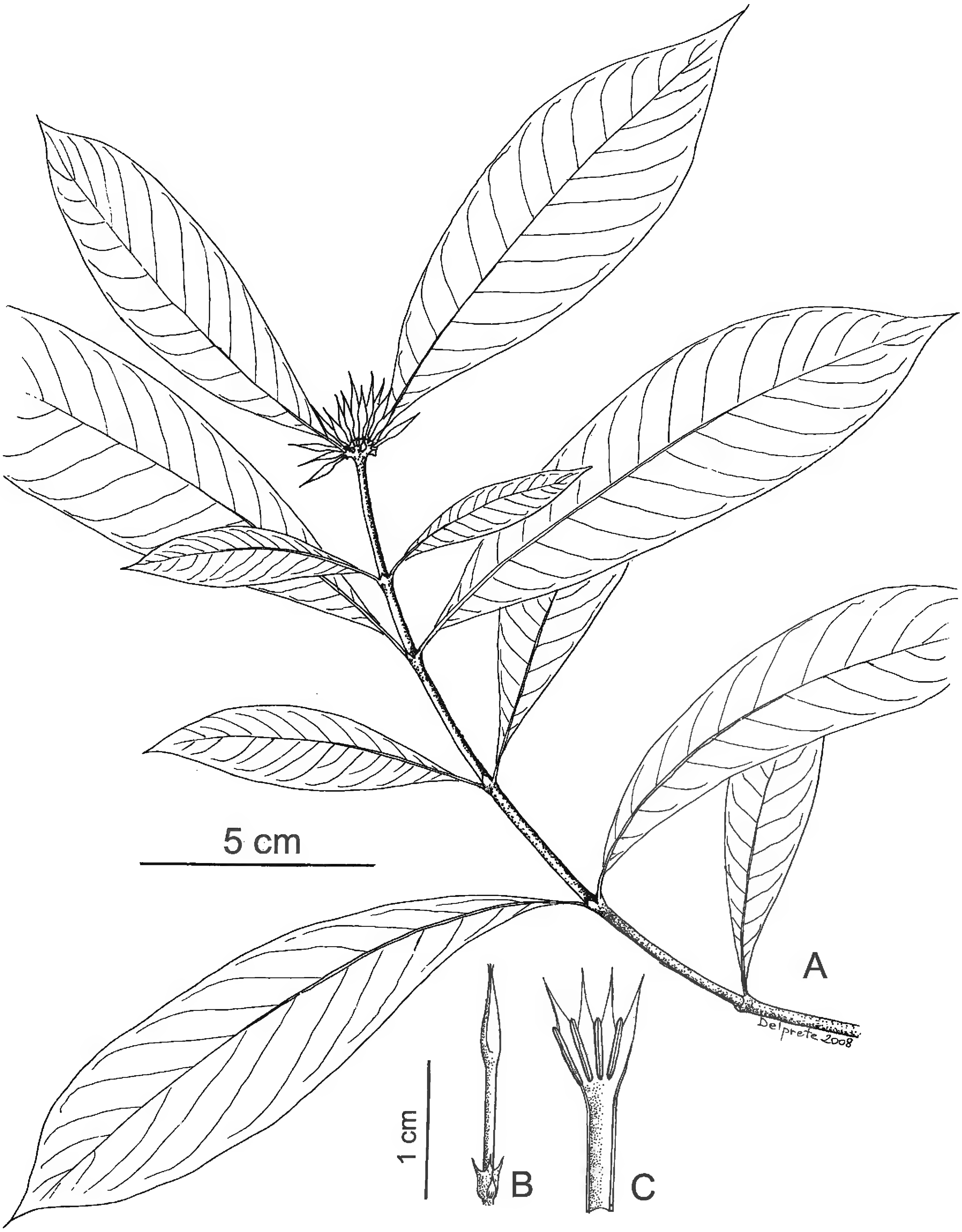

Fig. 1. *Ixora congestiflora* Delprete. A. Branchlet with terminal inflorescence. B. Flower bud. C. Open flower at anthesis. (from *Nogueira & Richter 692*, NY).

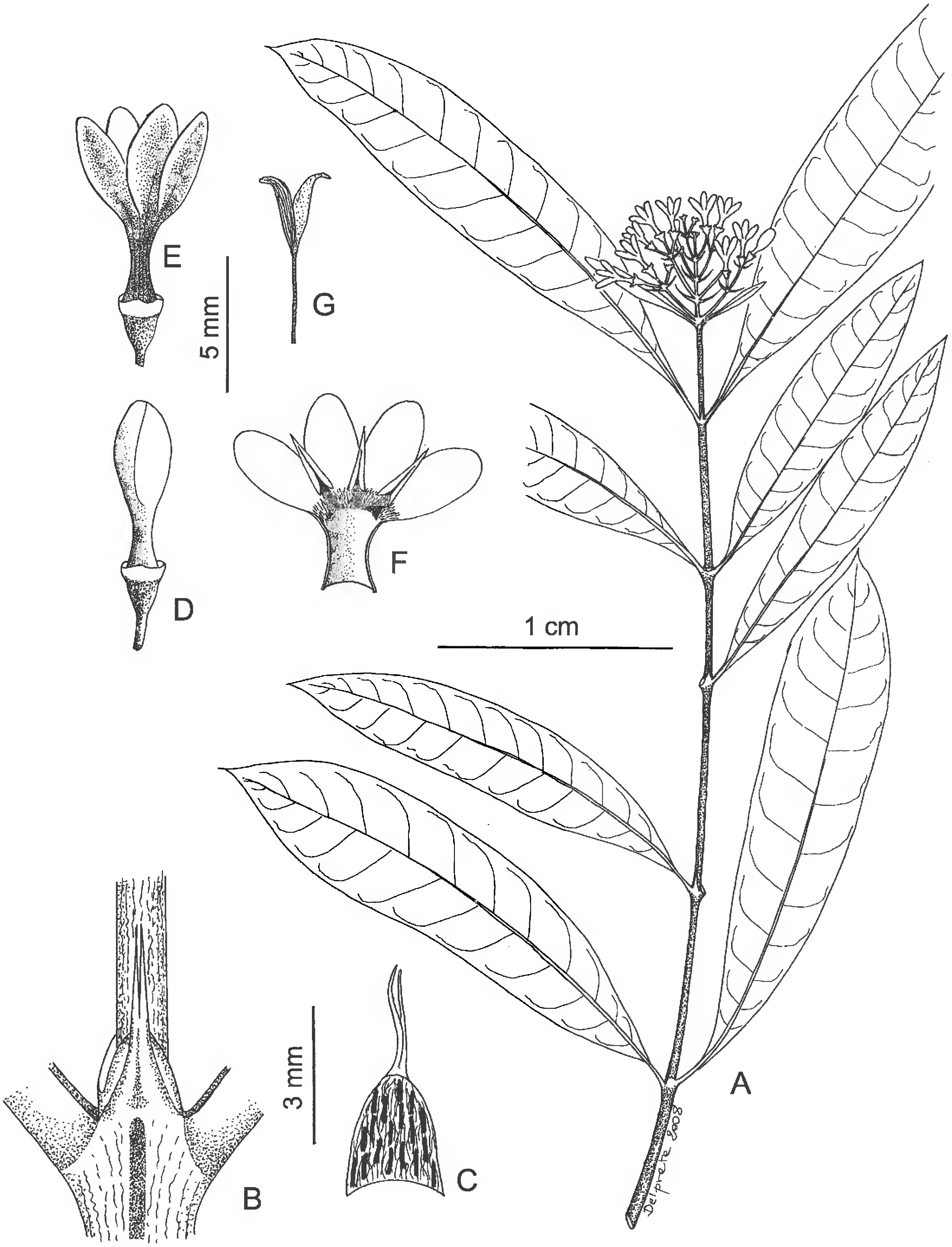

Fig. 2. *Ixora araguaiensis* Delprete. A. Branchlet with terminal inflorescence. B. Node with petiole bases and bifid stipule. C. View of adaxial face of stipule, showing pubescence and colleters. D. Flower bud. E. Flower at anthesis. F. Open flower at anthesis, with one anther removed. G. Style (from *M.A. da Silva et al. 4164*, NY).

Shrub ca. 1 m tall; branchlets glabrous. **Stipules** basally connate, 3.5–8 × 3–4 mm, base ovate to triangular, 1.5–2.5 mm long, arista 1.5–2.5 mm long, papyraceous, glabrous outside, densely sericeous-pubescent and intermixed with colleters inside. **Leaves** opposite, petiolate; petioles 7–15 mm long, glabrous; blades oblong-elliptic to oblong-oblanceolate, 7.5–11 × 1.7–3 cm, base acute to decurrent, apex obtuse to acute, or shortly acuminate (acumen, when present, deltoid, 3–5 mm long), subcoriaceous, glabrous throughout; secondary veins 10–15 each side, subsecondary veins reticulate (rarely subparallel) and 2–4 for each secondary vein. **Inflorescences** terminal, pedunculate, corymbose, erect-pubescent, with 2–4 pairs of lateral branches, 12–18-florous; branchlets 5–18 mm long, ending with three 3(4)-florous cymules; bracts subtending the cymules oblong-acuminate, 1.5–3 mm long; bracteoles 1 or 2 each flower, narrowly oblong, 0.5–1.5 mm long, glabrous. **Flower buds** with tube cylindrical, and ellipsoid in upper part (lobed portion), pale yellow. **Flowers** sessile or pedicellate; pedicels (when present) 1–3 mm long. **Hypanthium** obovoid, 1–1.3 mm long, glabrous or sparsely puberulent. **Calyx** cupular, 0.3–0.5 mm long, truncate or undulate, rarely with shallowly triangular lobes, glabrous. **Corolla** hypocrateriform, 7,5–8 mm long, white; tube gradually narrowing toward the middle, 3–3.5 mm long, 1–1.3 mm wide at base and at mouth (0.5–0.7 mm wide at middle portion), glabrous outside, sparsely pubescent at mouth internally; lobes elliptic-ovate, 4.5–5 × 1.7–2 mm, apex obtuse or round. **Stamens** exserted among the corolla lobes; anthers narrowly oblong, 1.8–2 mm long, acuminate. **Style** exserted well above the mouth, 6–7 mm long; style branches lanceolate, ca. 2 mm long. **Fruits** unknown.

Distribution and ecology.—Known only from the type material and an additional collection, near the Araguaia River, as an understory shrub growing in sandy soil, in northern Tocantins.

Observations.—To my knowledge, *Ixora araguaiensis* is unique within the genus because of its bifid stipules, as *Ixora* is traditionally characterized by stipules with one arista. In several other species, older stipules break up irregularly into two units, but this is not the case in *I. araguaiensis*, because its stipules have two aristae (sometimes basally connate) since very early stage (Fig. 2B–C). However, the consistency of this character within the species remains to be confirmed, as it is currently known from only two collections.

Conservation.—A rare species collected in the Parque Nacional do Araguaia, in the municipality of Pium. Although it was collected inside a national park, this species should be included in the category with imminent threat of extinction, due to the presence of large herds of cows grazing on the vegetation of this park, especially during the dry season (May–September).

Etymology.—The specific epithet of this taxon is dedicated to both the river and the national park where it was collected.

Taxonomic observations.—This species is similar to *Ixora brevifolia* Benth. (Delprete 2003, 2007) because of the terminal, corymbose to paniculate inflorescences, but differs by being a shrub ca. 1 m tall (vs. tree to 20 m tall in *I. brevifolia*), with 12–18-florous inflorescences (vs. 45–150-florous), corolla tube gradually narrowing toward the middle (vs. cylindrical) and leaf blades with 10–15 secondary veins each side (vs. 15–40 veins each side).

Additional specimen examined: **BRAZIL: TOCANTINS:** Araguaia River, right margin, between Rio Caiapó and Santana do Araguaia [Pará], várzea vegetation, 12 Aug 1978 (fl), *N.T. Silva 4800* (NY).

3. Ixora irwinii Delprete, sp. nov. (**Fig. 3**). TYPE: BRAZIL: TOCANTINS: 1 km S of Araguaína, at Rio das Lontras, 300 m, 15 Mar 1968 (fr), *H.S. Irwin, H. Maxwell & D.C. Wasshausen 21221* (HOLOTYPE: UB; ISOTYPE: NY).

Ixorae pubescenti Willd. ex Schult. & Schult. f. similis inflorescentiis terminalibus paniculatis et alabastris in parte summa fusiformibus, sed differt ramulis glabris (nec pubescentibus), laminis foliorum 4.5–11.5 cm longis (nec 18–30 cm longis) venis secundariis utrinque 10–15 (nec 20–25), rhachidi glabra (nec dense hirsuta), corollis 9–10 mm longis (nec 15–17 mm).

Shrub 0.8–1 m tall; branchlets glabrous. **Stipules** basally connate, 3.5–8 × 3–4 mm, base ovate, 2–3.5, arista 1.5–2.5 mm long, glabrous outside, densely sericeous-pubescent and intermixed with colleters inside. **Leaves** opposite, petiolate; petioles 7–15 mm long, glabrous; blades elliptic, oblong-elliptic to obovate, 4.5–11.5 × 1.5–4.5 cm, base acute to decurrent, apex obtuse to acute, or acuminate (acumen deltoid to narrowly triangular, 5–12 mm long), subcoriaceous, glabrous throughout; secondary veins 10–15 each side,

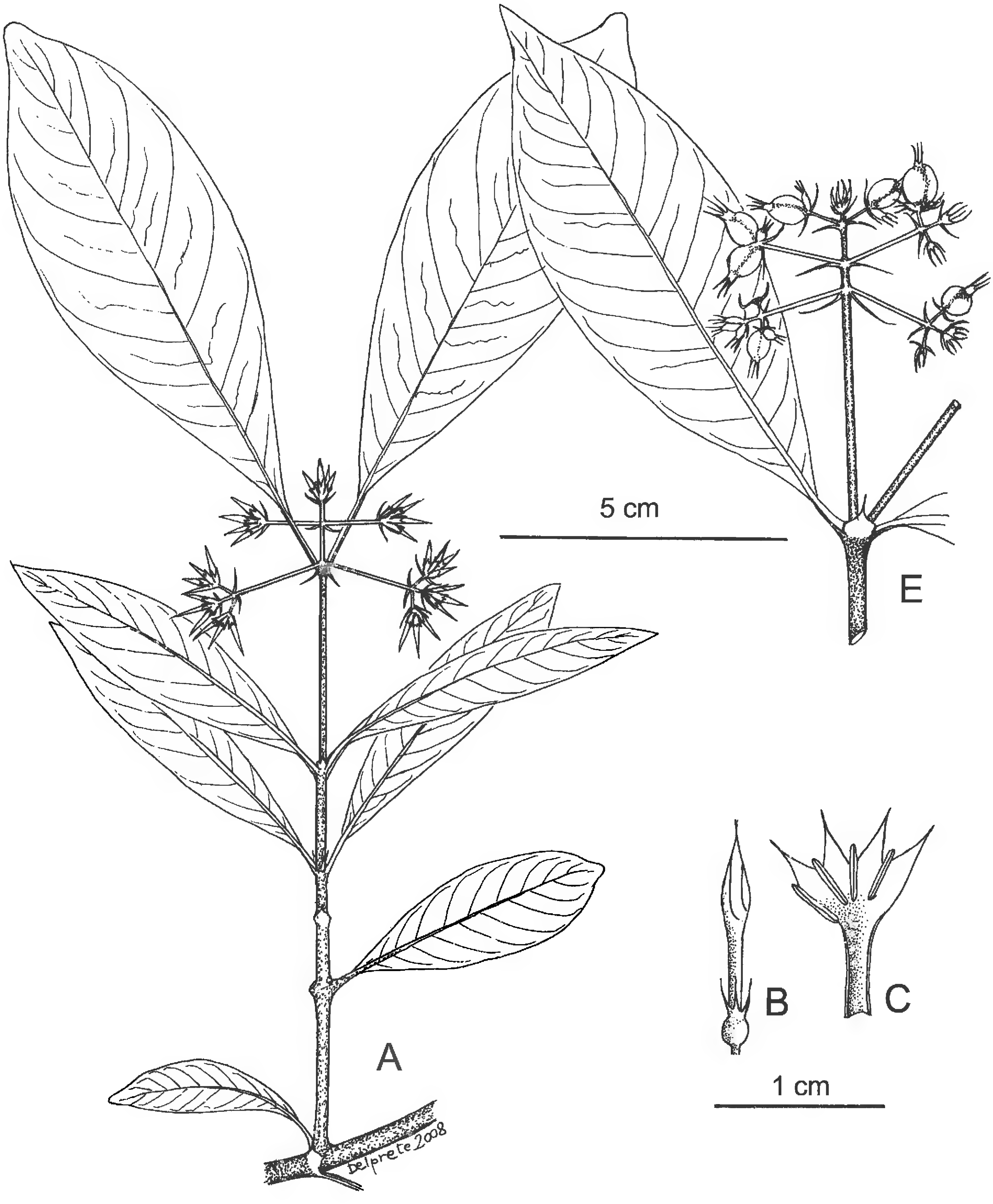

Fig. 3. *Ixora irwinii* Delprete. A. Branchlet with terminal inflorescence. B. Flower bud. C. Open flower at anthesis. D. Branchlet with terminal infructescence (A–D from *Neves et al. s.n.*, UFG 29847; E from *H.S. Irwin et al. 21221*, NY).

subsecondary veins parallel and about the same number as the secondaries. **Inflorescences** terminal, sessile or pedunculate, corymbose to short-paniculate, glabrous throughout, with 2–3 pairs of lateral branches, (27–)30–75-florous; branchlets 7–18 mm long, ending with three 5–7-florous cymules; bracts subtending the cymules ovate-acuminate, 2–3 mm long; bracteoles 1 or 2 each flower, ovate, 1.5–2.5 mm long, glabrous. **Flower buds** with tube narrowly cylindrical, and fusiform in upper part (lobed portion). **Flowers** sessile or subpedicellate; pedicels (when present) to 1 mm long. **Hypanthium** obovoid, ca. 1 mm long, glabrous. **Calyx** cupular; tube ca. 1 mm long; lobes 4, unequal, linear to acicular, 0.5–1.5 mm long, glabrous. **Corolla** hypocrateriform, 9–10 mm long, red externally, cream-white internally; tube narrowly-cylindrical, 4–4.5 × 0.5–0.7 mm, glabrous throughout; lobes narrowly-lanceolate, 4.5–5 × 1.7–2 mm, apex acuminate. **Stamens** exserted and reflexed among the corolla lobes; anthers oblong, 2.8–3 mm long. **Style** exserted just above the mouth, 5.5–6 mm long; style branches narrowly oblong, 0.5-0.7 mm long (not fully expanded). **Fruits** subglobose to oblong-ellipsoid, subdidymous, 6.5–7 × 5–5.5 mm, glabrous, passing from red to vinaceous to almost black at maturity.

Distribution and ecology.—Known only from a few collections as an undestory shrub growing in gallery forests of northern Tocantins.

Conservation.—A rare species in need of urgent protection because the few collections known are from areas without formal protection or from farm land.

Etymology.—The specific epithet of this taxon is dedicated to Howard Irwin, indefatigable collector who worked for the New York Botanical Garden, organized and carried out the project *Flora of the Brazilian Planalto* during 1964–1975, and is the first collector of this species.

Additional specimens examined: **BRAZIL. Tocantins:** Faz. Neto, Rio Água Boa, 8°12'52"S, 48°09'57"W, 12 Jan 2001 (fl), *S.F. Lolis et al. 213* (HTO, UFG); Mun. Tanqueira, floresta de galeria, 8°11'49"S, 48°08'48"W, 16 Dec 2001 (fl), *S.F. Lolis et al. 357* (HTO, UFG); Mun. Paraíso do Tocantins, Fazenda Uberaba, 10°09'36"S, 48°55'32"W, 14 Dec 1999 (fl), *Neves et al. s.n.* (HTO 7405).

Taxonomic observations: This species is similar to *Ixora pubescens* Willd. ex Schult. & Schult. f. in Roem. & Schult. because of the terminal, paniculate inflorescences and flower buds fusiform in the upper part (lobed portion), but differs by having glabrous vegetative branchlets (vs. puberulent in *I. pubescens*), leaf blades 4.5–11.5 cm long (vs. 18–30 cm long) with 10–15 secondary veins each side (vs. 20–25 secondary veins each side), glabrous rachis (vs. densely hirsute), and corollas 9–10 mm long (vs. 15–17 mm long).

KEY TO THE NATIVE SPECIES OF *IXORA* IN THE STATES OF GOIÁS AND TOCANTINS, BRAZIL

1. Inflorescence very compact, with branches 1-2 mm long ____ **I. congestiflora**
1. Inflorescence not as compact, with branches more than 7 mm long.
   2. Flower buds oblong-ellipsoid in upper part (tip round to obtuse).
      3. Shrub ca. 1 m tall; leaf blades with 10–15 secondary veins on each side; inflorescence 12–18-florous; corolla tube gradually narrowing toward the middle ____ **I. araguaiensis**
      3. Tree to 20 m tall; leaf blades with 15–40 secondary veins on each side; inflorescence 45–150-florous; corolla tube cylindrical ____ **I. breviflora**
   2. Flower buds fusiform in upper part (tip acute to acuminate).
      4. Vegetative branchlets glabrous; leaf blades 4.5–11.5 cm long, with 10–15 secondary veins on each side; rachis glabrous; corollas 9–10 mm long ____ **I. irwinii**
      4. Vegetative branchlets puberulent; leaf blades 18–30 cm long and with 20–25 secondary veins on each side; rachis densely hirsute; corollas 15–17 mm long ____ **I. pubescens**

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LASIAMBIX DOMINICENSIS GEN. AND SP. NOV., A EUDICOT FLOWER IN DOMINICAN AMBER SHOWING AFFINITIES WITH FABACEAE SUBFAMILY CAESALPINIOIDEAE

George O. Poinar, Jr.
Department of Zoology
Oregon State University
Corvallis, Oregon 97331, U.S.A.

Kenton L. Chambers
Department of Botany and Plant Pathology
Oregon State University
Corvallis, Oregon 97331, U.S.A.

Alex E. Brown
629 Euclid Avenue
Berkeley, California 94708, U.S.A.

ABSTRACT

Lasiambix dominicensis gen. & sp. nov., represented by six floral specimens at different stages of development, is described from Tertiary Dominican amber. The genus is characterized by small, perigynous, bilaterally-symmetrical flowers possessing a cup-shaped hypanthium, 5 ovate-deltate sepals, 5 equal, early-deciduous petals, 3 short, incurved stamens, each attached to the hypanthial cup opposite a sepal, and a superior, simple pistil attached basally within the hypanthium, the style positioned excentrically opposite the stamens and between 2 of the sepals. Immature fruits are obovoid, with a short, thick stipe and rugose surface. The combination of floral traits suggests a position in Fabaceae subfamily Caesalpinioideae, but with uncertain tribal affinity.

Key Words: amber, Dominican Republic, Caesalpinioideae, eudicot flower, Fabaceae, Greater Antilles, Tertiary

RESUMEN

Se describe **Lasiambix dominicensis** gen. & sp. nov., representado por seis especimenes florales en diferente estado de desarrollo, del ámbar terciario dominicano. El género se caracteriza por sus flores pequeñas, periginas, con simetría bilateral, con un hipanto en forma de copa, 5 sépalos ovado-deltados, 5 pétalos iguales, tempranamente caducos, 3 estambre cortos, incurvados, adheridos a la copa del hipanto opuestos a los sépalos, y un pistilo súpero, simple unido basalmente al hipanto, El estilo excéntrico opuesto a los estambres y entre dos de los sépalos. Los frutos inmaduros son obovoides, con un estipe corto y grueso, y superficie rugosa. La combinación de trazos florales sugiere una posición en las Fabaceae subfamilia Caesalpinioideae, pero con una afinidad tribal incierta.

INTRODUCTION

Amber is well known for its preservative qualities of both animal and plant remains (Poinar 1992, Poinar & Poinar 1999). Amber flowers, maintained in three-dimensional form, are often preserved with such detail that they can be assigned to extant genera (Spahr 1993). Such fossils can be useful in paleontological reconstructions (Poinar & Poinar 1999).

The majority of described amber flowers originate from Baltic deposits (Spahr 1993); however legume (Dilcher et al. 1992; Poinar 1991) and palm (Poinar 2002a, 2002b) flowers have been described from Dominican amber, and there are also descriptions of Early Cretaceous flowers in Burmese amber (Poinar & Chambers 2005; Poinar et al. 2007).

During an ongoing investigation of floral remains in Dominican amber, 6 flowers in 5 separate pieces of amber were discovered, which could be linked through the possession of an identical cup-shaped, puberulent hypanthium with deltate-ovate, spreading-recurved sepals. One flower, with petals present, is probably at a pre-anthesis stage; 3 flowers, with petals absent, are at or near anthesis; and 2 flowers show early fruit development, with the stipe of the pod still held in the hypanthium. The exceptional preservation of the flowers and clarity of the amber allow description and photographic documentation of their unique features. These flowers, which are described below as a new genus, possess a combination of characters that favors an assignment to Fabaceae subfamily Caesalpinioideae.

MATERIALS AND METHODS

All 5 pieces of amber containing the fossil flowers originated from mines in the northern mountain range (Cordillera Septentrional) of the Dominican Republic, between the cities of Puerto Plata and Santiago. Dating of Dominican amber is controversial, with the youngest proposed age of 20–15 mya based on foraminifera (Iturralde-Vincent & MacPhee 1996) and the oldest as 45–30 mya based on coccoliths (Cêpek in Schlee 1999). Most of the amber is secondarily deposited in turbiditic sandstones of the Upper Eocene to Lower Miocene Mamey Group (Draper et al. 1994).

The 6 flowers are similar in the morphology of their floral cup (hypanthium) and are assumed to have originated from the same plant species. The amber piece containing the flower assigned to catalogue number Sd-9-154A (Holotype) is circular in outline, measures 13 mm in diameter, 9 mm in greatest thickness and weighs 6 grams. The amber piece containing specimen Sd-9-154B is roughly triangular in shape, measures 12 mm along the sides, 7 mm at the base, is 3 mm thick and weighs 3 grams. The third amber piece (Sd-9-154C) is rectangular, measures 8 mm by 7 mm along the sides, 2 mm in thickness and weighs 2 grams. The fourth amber piece (Sd-9-154D), which contains the specimen with the petals, is semicircular in outline, measures 17 mm in greatest length, 9 mm in greatest width, 7 mm in greatest thickness and weighs 1 gram. The fifth amber piece (Sd-9-154E), which contains the specimen with the fruits, is trapezoidal in outline, measures 17 mm in greatest length, 12 mm in greatest width, 8 mm in greatest thickness and weighs 1 gram. All specimens are deposited in the Poinar amber collection maintained at Oregon State University.

DESCRIPTION

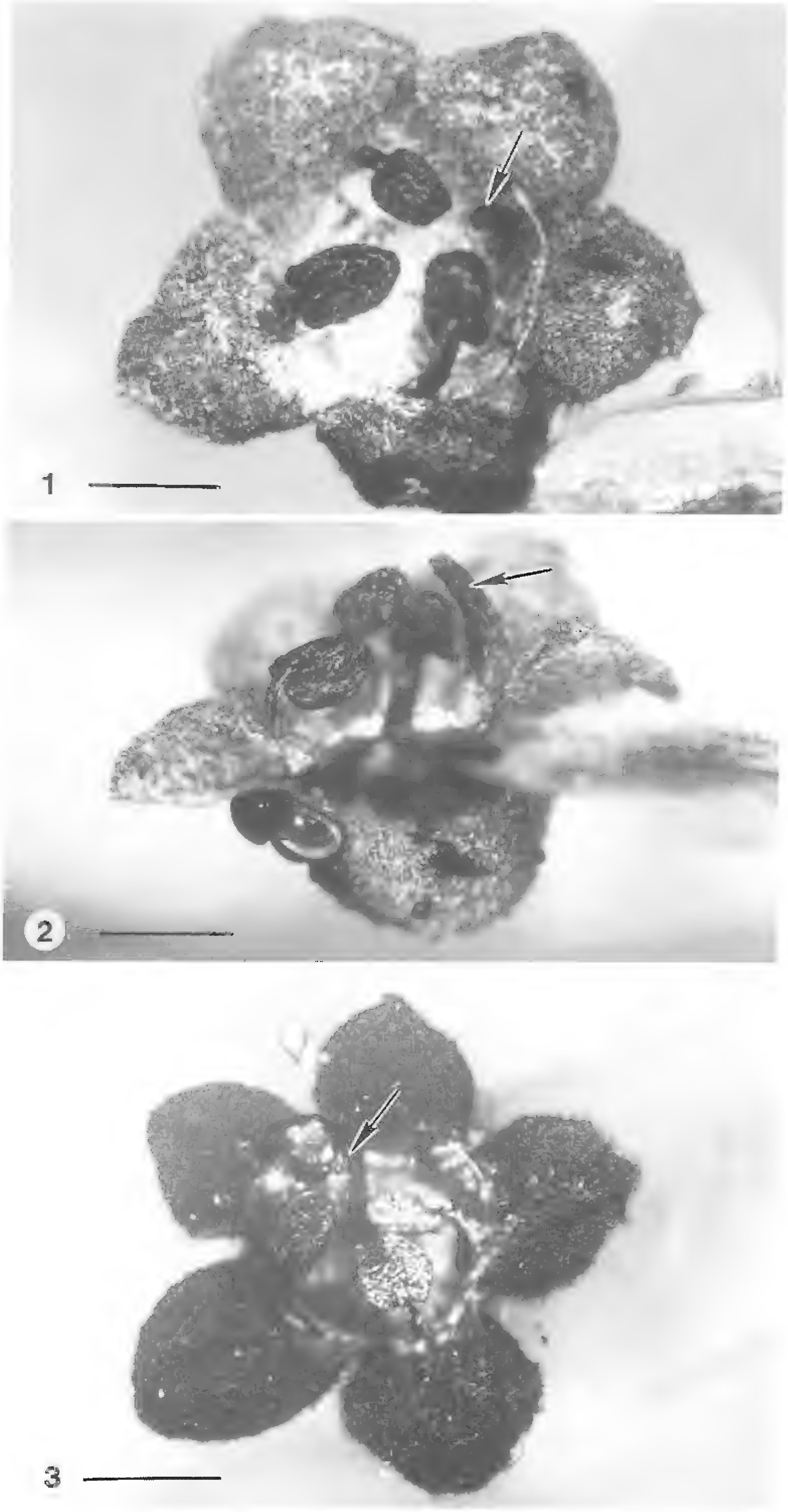
Lasiambix Poinar, Chambers & Brown, gen. nov. Type species: *Lasiambix dominicensis* Poinar, Chambers & Brown sp. nov.

Flowers small, bilaterally symmetrical, perfect (bisexual), with a cup-shaped hypanthium; calyx isosepalous, sepals 5, deltate-ovate, free, imbricate or valvate; corolla isopetalous, petals 5, free, early-deciduous; stamens 3, arising from rim of hypanthium opposite 3 adjacent sepals, filaments short, linear, strongly incurved, anthers bilocular, dorsifixed, introrse; ovary superior, sessile at base of hypanthial cup; style single, barely exceeding stamens, positioned excentrically opposite the stamens and between the two sepals that lack stamens; stigma simple, not enlarged; fruit (immature) obovoid, tapered to a short, thick stipe, style deciduous.

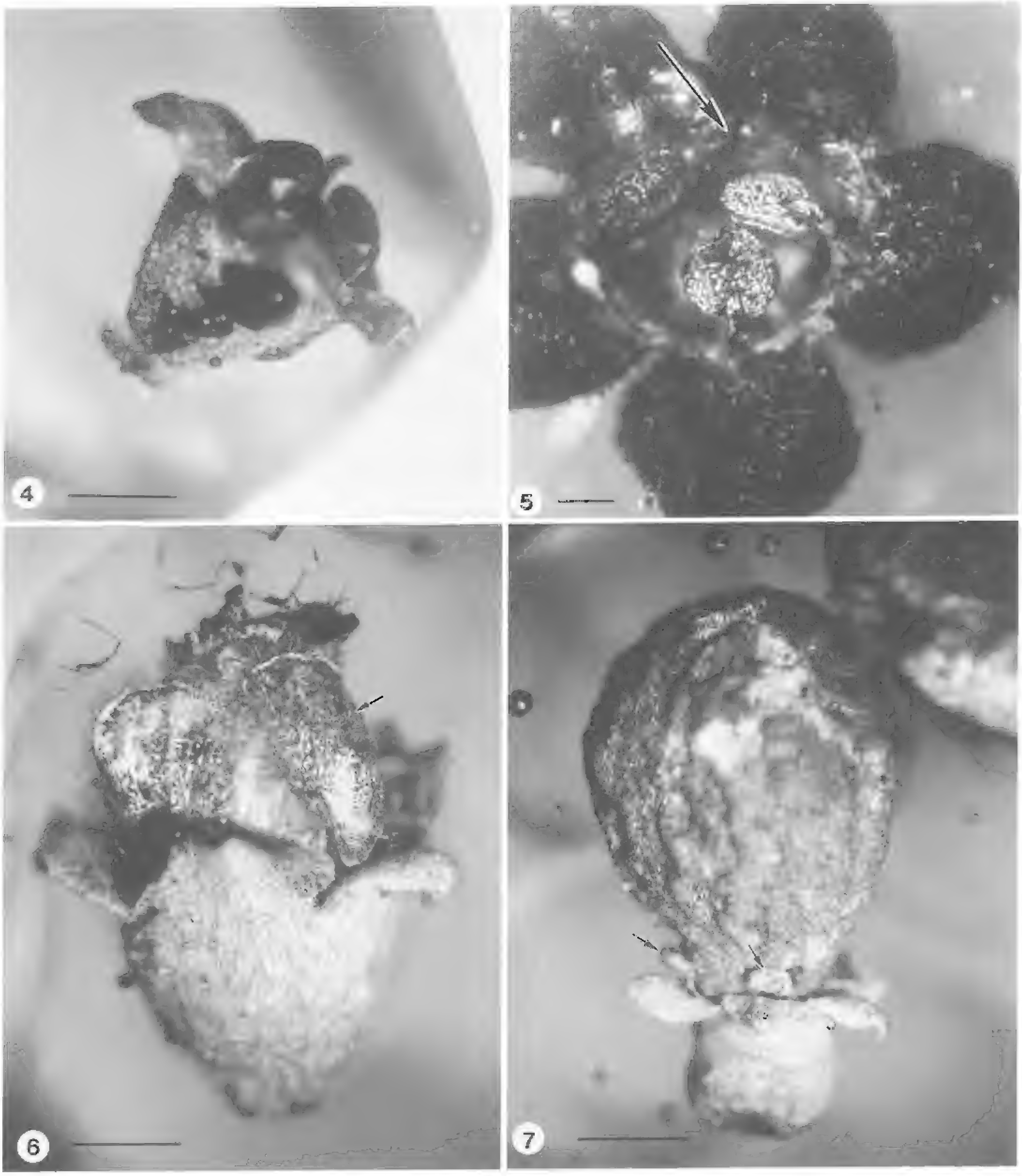
Lasiambix dominicensis Poinar, Chambers & Brown, sp. nov. **(Figs. 1–9)**. Type: HISPANIOLA. Dominican Republic: amber mine in the northern mountain ranges (Cordillera Septentrional), between Puerto Plata and Santiago, 2003, collector unknown (holotype: OSC-cat. no. Sd-9-154A, Poinar amber collection).

Flowers 3.6–3.7 mm in diameter, bilateral, pedicel none; hypanthium cup-shaped, densely tomentulose externally, pubescent within, 1.7–2.1 mm long, the opening 1.4–2.2 mm wide, bearing a distinct rim to which stamens and petals are attached; disc none; sepals deltate-ovate, densely tomentulose on both surfaces, spreading with reflexed tip, 0.9–1.6 mm long, 1.0–1.6 mm at widest point; petals erect, early-deciduous, 1.3–1.9 mm long, 0.8–1.1 mm wide, oblanceolate, bluntly rounded at tip, thick-textured, margins ciliate; stamens short, incurved, slightly exserted from hypanthium, the filaments attached to hypanthial rim, linear, thickened at point of insertion, glabrous, the anthers positioned horizontally over the mouth of hypanthium, bilocular, slightly dorsifixed, ovate, blunt-tipped, cordate at base, 0.4–0.7 mm long, glabrous, dehiscence introrse by lengthwise slits; ovary sessile in hypanthial cup, lightly pubescent, style linear, 0.6–1.0 mm long, pubescent proximally, stigma terminal, undivided, not enlarged; fruit (immature) obovoid, probably 1-few-seeded, 4.8–4.9 mm long, 3.7–3.9 mm wide, the short, thick stipe mostly enclosed in the hypanthium, surface thick-textured and rugose (as preserved), style not persistent.

Etymology.—Genus name from the Greek "lasios," woolly, and "ambix," cup, referring to the tomentulose hypanthium that unifies the 6 specimens. Species name derived from the Dominican Republic, the country where the fossils were found.



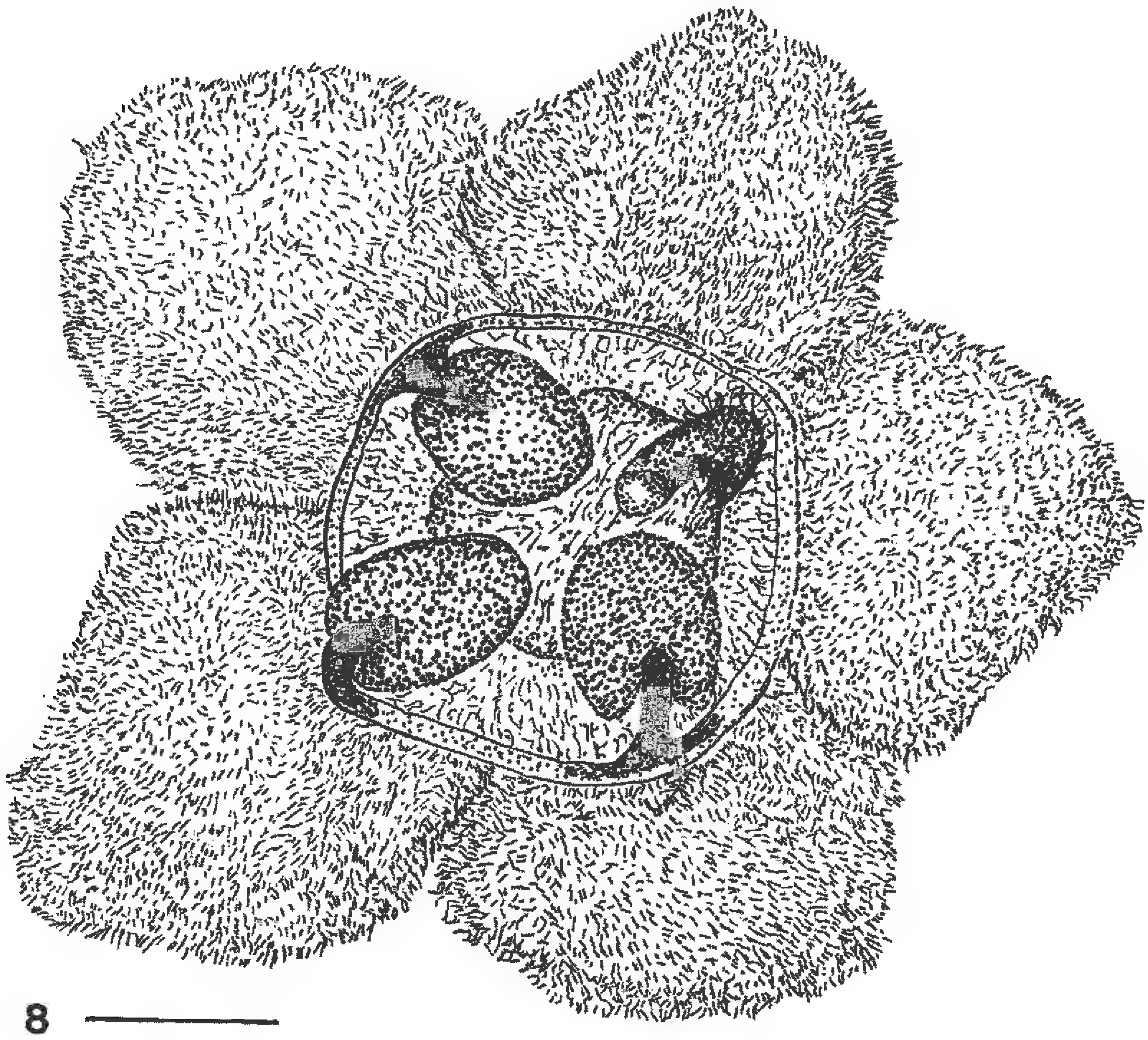
Figs. 1–3. *Lasiambix dominicensis* gen. and sp. nov. 1. Top view of holotype (accession # Sd-9-154A); arrow points to style. Scale bar = 0.82 mm. 2. Oblique view of holotype (accession # Sd-9-154A); arrow points to style. Scale bar = 0.82 mm. 3. Top view of specimen Sd-9-154C; arrow points to style. Scale bar = 0.82 mm.



Figs. 4–7. *Lasiambix dominicensis* gen. and sp. nov. 4. Side view of holotype (accession # Sd-9-154A). Scale bar = 0.84 mm. 5. Detail of stamens in specimen Sd-9-154C; arrow points to style. Scale bar = 0.28 mm. 6. Side view of specimen Sd-9-154D; arrow points to loose petal. Scale bar = 0.77 mm. 7. Side view of specimen Sd-9-154E showing developing fruit; note stamens at base (arrows). Scale bar = 0.57 mm.

DISCUSSION

The floral features that we believe unite these 6 specimens into a single taxon are evident in the photographic illustrations (Figs. 1–7). Although at different stages of development, the flowers have a remarkably similar hypanthium, with respect to shape, calyx lobes, and pubescence. All have a truncate base where they broke off of their inflorescences. One specimen with an immature fruit (Fig. 7) retains a pair of stamens attached



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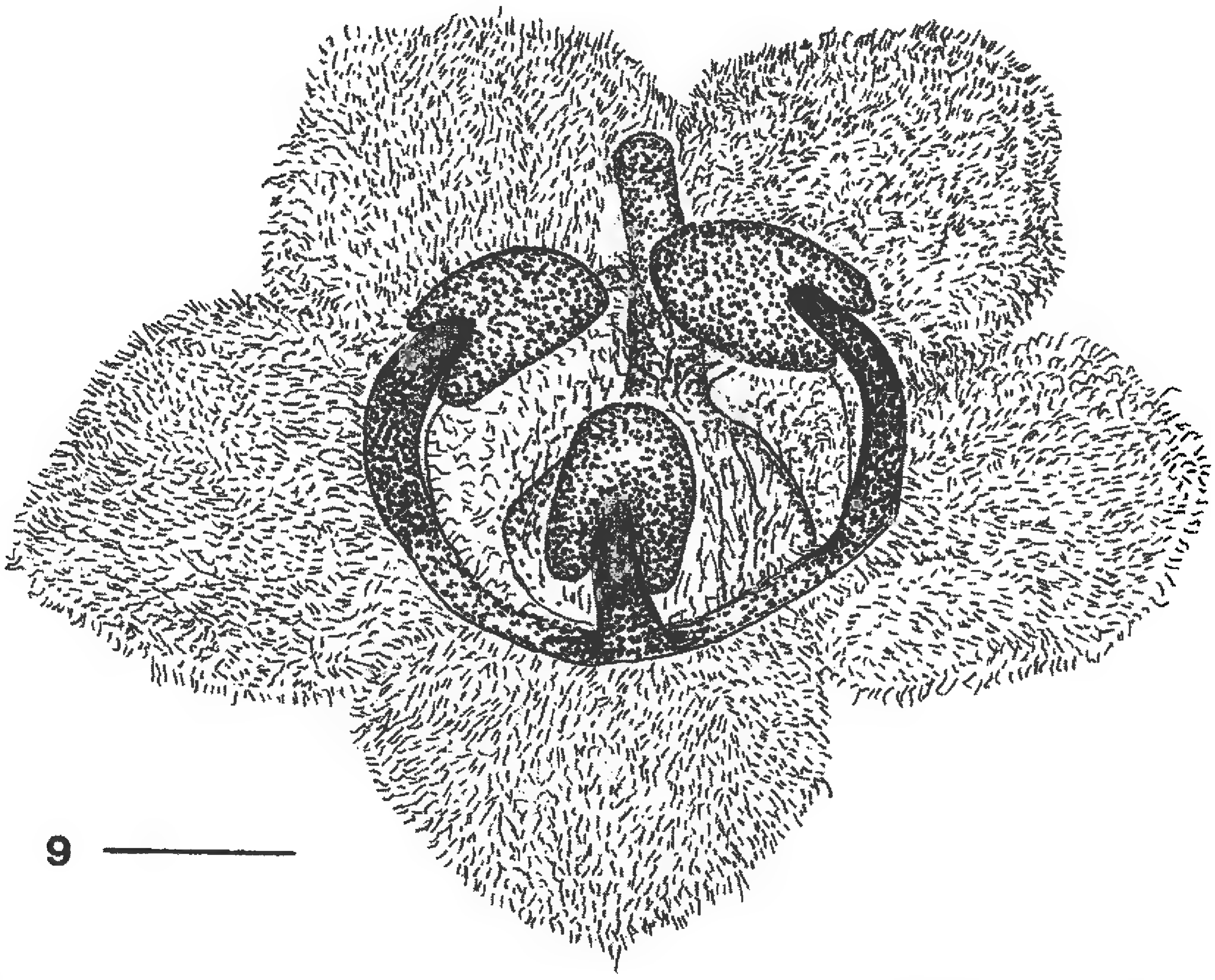

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FIGS. 8–9. Holotype of *Lasiambix dominicensis* gen. and sp. nov. (accession # Sd-9-154A). 8. Top view. Scale bar = 0.57 mm. 9. Oblique view. Scale bar = 0.57 mm.

opposite the calyx lobes. The specimen in early flower (Sd-9-154D, Fig. 6) has all 5 petals visible, and one is detached at the base, illustrative of what we term an early-deciduous corolla. The petals are clearly seen when the specimen is viewed from the top as well as the sides. The center of this flower is unsuitable for study due to an accumulation there of apparent insect remains and frass. The sharp hypanthial rim on the 3 flowers at or near anthesis shows where the petals presumably were attached, alternate with the sepals. It remains ambiguous whether the sepal lobes were imbricate or valvate in the bud, perhaps because of different degrees of spreading and separation in the samples at hand. Because no slits or pores are evident on the back, sides, or tips of the anthers, we suggest an introrse dehiscence, which is supported by observations of the adaxial side of one strongly inflexed stamen. The nature of the mature fruit is uncertain, although from the shape and thick-textured exocarp of the 2 specimens here (Fig. 7), a non-compressed, 1- or few-seeded drupaceous fruit is suggested. Although atypical for members of the Fabaceae, several extant genera of the Cassieae have similar indehiscent, drupaceous fruits. *Dialium* s.l. is characterized by small fruits consisting of one seed surrounded by a soft, but somewhat dry, edible aril (Gentry 1993). Few-seeded, ovoid, fleshy- or thick-walled fruits are not unusual in Fabaceae subfamily Caesalpinioideae (e.g. Lewis et al. 2005). This fruit-type, together with a well-developed hypanthium, a superior simple pistil, regular corolla, reduced stamen number, and a zygomorphy of androecium and pistil, are what lead us to suggest assigning the fossil to this family and subfamily.

The caesalpinioid legumes are extremely diverse in floral characteristics, including numbers of stamens, presence or absence of a hypanthium, numbers and form of petals, length of filaments, form of anthers and stigmas, shape and structure of fruits, floral symmetry, modification to unisexuality, etc. The compendium by Polhill and Raven (1981), with its taxonomic treatments of the relevant tribes (Cowan & Polhill 1981; Irwin & Barneby 1981; Polhill & Vidal 1981), was consulted in a search for modern genera with the particular combination of features seen in the fossils. Illustrations and descriptions of genera were examined in Taubert (1894), Hutchinson (1964), and Lewis et al. (2005). No examples have been found that correspond in all respects with *Lasiambix*, but its described traits are present separately in numerous caesalpinioid genera.

A cup-shaped, externally puberulent hypanthium occurs frequently in the subfamily. Bilateral symmetry (zygomorphy) is also common, and this accompanies a reduction to three stamens in such genera as *Tamarindus*, *Macrolobium*, *Gilbertiodendron*, *Elizabetha*, *Apuleia*, *Dialium*, etc. As discussed by Tucker (1998, 2002) there are parallel evolutionary trends towards reduction of stamen number in groups of related genera in separate tribes (her examples were Detarieae-Amherstieae and Dialiinae). From the basic number 10, stamens may be reduced to as few as 1 (some *Dialium* spp.), and during development, some of the stamen primordia that form early may cease their growth and become rudimentary or staminodial (e.g. *Gilbertiodendron*, *Macrolobium*; Tucker 2002). Except for *Dialium* and *Apuleia*, the 3-stamen genera mentioned fall into the Amherstieae (including Macrolobieae) clade, as defined by analysis of the chloroplast *trn*L intron (Bruneau et al. 2001). This group is also recognizable in the *rbc*L analyses by Doyle et al. (1997) and Kajita et al. (2001). However, the corolla evolution in these particular genera leading to loss of all but one petal to form an adaxial vexillum (e.g. Cowan 1953) , the 2-many-seeded, mostly dehiscent pods, plus the usual absence of a hypanthium, argue against a relationship to *Lasiambix*. *Cynometra*, also in this clade, is discussed below.

Dialium and *Apuleia*, of subtribe Dialiinae, show some resemblance to *Lasiambix* in their zygomorphic, few-stamened flowers and their few-seeded, indehiscent fruits. According to Irwin and Barneby (1981, p. 101) *Dialium* "can be defined accurately and rigorously by its pod, a sort of indehiscent, 1- or 2-seeded nut, sometimes strongly, sometimes scarcely compressed laterally, consisting of a crustaceous exocarp and a pulpy, when ripe mealy endocarp enveloping the seeds." In their key (p. 100) the fruit is termed "drupaceous." The flowers of *Dialium*, a pantropical genus, are hypogynous and have only 1 or 2 petals and usually 2 stamens. The related *Apuleia*, of South America, possesses a hypanthium and 3 stamens, but its pistil is exserted, not sessile, its perianth is 3-merous, and its pod is compressed and coriaceous, not ovoid. Despite

their few-seeded, indehiscent pods, neither of these few-stamen genera of Dialiinae suggests a close affinity to *Lasiambix*.

Other possible relationships of the fossils are with genera having regular flowers and more numerous stamens but with a similar type of few-seeded fleshy fruit. One such example is *Vouacapoua* of tribe Caesalpinieae (Lewis et al. 2005). This genus possesses regular flowers with 10 short stamens, but its hypanthium, sepals, and short petals much resemble *Lasiambix*, and its fruits are round, thick-walled, 1-seeded, and dehisce by a single furrow (Lewis et al. 2005, p. 161; Polhill & Vidal 1981, p. 89). The genus is presumed to have affinity to the *Peltophorum* group of tribe Caesalpinieae (Bruneau et al. 2001; Haston et al. 2003), but as yet the DNA support for this connection is weak.

A similar type of fruit occurs in the large genus *Cynometra* of tribe Detarieae (Lewis et al. 2005, p. 89). Its pod is described as thick, turgid, rugose to verrucose (rarely smooth), 1-seeded, and regularly indehiscent with a spongy pericarp (Hutchinson 1964, p. 235; Dwyer 1958); it lacks a floral disc, its ovary is usually hairy, and its style may be eccentric in the hypanthium (Dwyer 1958, p. 322). However, it has 10 long-exserted stamens, a shorter hypanthium, and a usually showier perianth than in *Lasiambix* (Dwyer 1958). Other differences, besides these, are that its sepals are glabrous adaxially (except *C. cubensis* Rich.) and its filaments are united very briefly at the base. Modern-day *Arcoa*, of Hispaniola, has turgid, 1-seeded, indehiscent fruits (Lewis et al. 2005, p. 132), but its flowers differ considerably from *Lasiambix* in being unisexual, bearing ca. 12 stamens, and having an exserted pistil with capitate stigma (Herendeen et al. 2003). Another Caribbean genus, *Stahlia* (tribe Caesalpinieae), has fleshy, 2-seeded, indehiscent fruits, regular 5-merous perianth, imbricate sepals, and well-developed, dorsally puberulent petals (Hutchinson 1964, p. 235; Lewis et al. 2005, p. 145). It differs from *Lasiambix* principally in having 10 erect, connivent stamens with filaments densely woolly in the lower half. Placement of *Stahlia* near the large genus *Caesalpinia* and its segregates was established by the molecular and morphological studies of Simpson et al. (2003).

The examples mentioned, falling into several distinct clades within the subfamily, illustrate the parallelisms in floral and fruit morphology that make it difficult to suggest a specific, definitive placement of *Lasiambix*. A large amount of recent phylogenetic research, both morphological and molecular, was reviewed by Lavin et al. (2005), to estimate the time frame of early diversification of this and other subfamilies of Leguminosae. Earlier estimates of a Late Cretaceous origin of the family and a "basal" position for Caesalpinioideae (e.g. Polhill et al. 1981; Herendeen et al. 1992), are no longer accepted as "conventional wisdom." Rather, the fossil record supports an origination in the Paleocene, allowing some 60 my for diversification within the family (Lavin et al. 2005). In molecular phylogenetic studies, with best resolution provided by the *mat*K chloroplast gene, divergence of 6 early-formed lineages of caesalpinioids was found, along with the similarly old crown nodes of many papilionoid and mimosoid clades. Caesalpinioids are viewed as a paraphyletic grade from which stem the mimosoids and papilionoids, but because of the very early, rapid branching of the ancestors of modern clades, the caesalpinioid grade "harbor(s) neither the oldest diversification nor some other quality of legume antiquity" (Lavin et al. 2005).

If our suggested placement of *Lasiambix* is correct, it offers a well-preserved example of several specialized floral characteristics of Tertiary-age caesalpinioid legumes. These include the loss of all but 3 stamens and accompanying bilateral symmetry of the flowers, an absence of petals at anthesis, and presence of few-seeded, fleshy, probably indehiscent fruits. What pollination syndrome is represented by flowers with short, incurved stamens and no apparent nectar disc, is difficult to say. Perhaps nectar was produced at the base of the ovary, which was not visible to us. In this case small bees might have been able to enter the flowers and remove pollen from the arched, introrse anthers. The ecology of the plants is likewise unknown, other than that they grew in proximity to *Hymenaea* in moist tropical forests such as those described by Poinar and Poinar (1999). Such habitats are typical for many genera of modern-day Caesalpinioideae.

Note: In the illustrations, because the orientation of the flowers is unknown, we have not tried to suggest a placement of the stamens as either abaxial, as in *Macrolobium* et al. (Cowan 1953) or adaxial as in *Dialium* et al. (Tucker 1998).

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BOOK NOTICE

CARLOS RODIRÍGUEZ RAMÍREZ. 2007. **Chipinque: Testigo de la Naturaleza.** (ISBN 978-970-9715-42-2, hbk.). Fondo Editorial de Nuevo León, Zaragosa 1300 sur, Edificio Kalos, Nivel C2, Local 202, CP 64000 Monterrey, Nuevo León, Mexico. (**Orders:** www.fondoeditorialnl.gob.mx, (81) 8344 2970 y 71). $150.00, 351 pp., color photographs, 10.5" x 14".

Spanish-text, coffee-table style book with hundreds of wonderful color photographs highlighting the ecology and natural beauty of Chipinque Park in Monterrey, Nuevo León, Mexico. The table of contents is listed below.

1. Introducción
2. Historia: el devenir de Chipinque
3. Chipinque: el parque ecológico
4. Entorno natural: hidrología, geología y clima
5. Ecosistemas de Chipinque (Matorral submontano, Matorral rosetófilo, Bosque de encino, Bosque de pino, Bosque mesófilo de montaña)
6. Fauna de Chipinque (Insectos, Arácnidoa, Reptiles, Aves, Mamíferos)
7. Bibliografía
8. Agradecimientos

KRUSCHKE NAMES IN NORTH AMERICAN *CRATAEGUS* (ROSACEAE): A CORRECTION AND CLARIFICATIONS

J.B. Phipps

The University of Western Ontario
Department of Biology
1151 Richmond St. N.
London, Ontario
N6A 5B7, CANADA
jphipps@uwo.ca

In a recent paper (Phipps 2007) I inadvertently stated an incorrect collection date for the holotype of *Crataegus pisifera* Sarg. It should be 28 September 1901 rather than 26 July 1901 as recorded in Phipps (2007). The remainder of the commentary on *C. pisifera* in that paper stands, however.

With respect to the same paper, communication with the nomenclature specialist at Harvard University, Kanchi Gandhi, indicated to me that I was in error in designating two lectotypes, as the names with which I was dealing had never been validly published. Since 1 January 1958, in order to be validly published, names must have a type indicated and a type must be a single specimen (see Vienna Code Art. 37.1, 8.1 and 8.2). However, the two names below were designated with a "type" representing specimens from different gatherings. Thus, in order to validate Kruschke's names, holotypes rather than lectotypes should have been designated. Accordingly, the two names are validly published below with appropriate holotypes designated. It may also be noted that were I to have ascribed the names to myself the citations of the relevant names would have been 'J.B. Phipps' but I retain 'Kruschke,' also permissible, therefore accepting Kruschke as the author since he provided the validating Latin diagnoses (Art. 46.2).

1. Crataegus mollis (Torr. & A. Gray) Scheele var. **incisifolia** Kruschke, var. nov. Type: U.S.A.: Wisconsin: Rock Co.: Avon, along Sugar River, 27 May 1947, *E.P. Kruschke K-47-8* (holotype: MIL; isotype: A).

Comment.—Kruschke (Milwaukee Public Mus. Public. Bot. 3:128. 1965) cited two collections from May and September 1947, respectively.

2. Crataegus schuettei Ashe var. **gigantea** Kruschke, var. nov. Type: U.S.A. Wisconsin: City of Milwaukee, north side, 16 Sep 1942, *E.P. Kruschke K-42-288* (holotype: MIL; isotype: A).

Comment.—Kruschke (Milwaukee Public Mus. Public. Bot. 3:75. 1965) cited three collections from Sep 1942, May 1943, and Feb 1944, respectively.

ACKNOWLEDGMENTS

I thank Kanchi Gandhi (GH) and John McNeill (E) for nomenclatural advice.

REFERENCE

Phipps, J.B. 2007. Kruschke names in North American *Crataegus* (Rosaceae). J. Bot. Res. Inst. Texas. 1:1011-1014.

BOOK NOTICE

David W. Roubik, Shoko Sakai, and Abang A. Hamid (eds.). 2005. **Pollination Ecology and the Rain Forest, Sarawak Studies, Ecological Studies Series, Vol. 174.** (ISBN 0-387-21309-0, hbk.; ISSN 0070-8356). Springer Science + Business Media, Inc., 233 Spring Street, New York, New York 10013, U.S.A. (**Orders:** www.springer.com, service-ny@springer.com, 1-800-SPRINGER). $139.00, 307 pp., 79 illustrations, 12 color plates, 6" × 9 1/2".

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THOMAS WALTER TYPIFICATION PROJECT, V: NEOTYPES AND EPITYPES FOR 63 WALTER NAMES OF GENERA D THROUGH Z

Daniel B. Ward

Department of Botany
University of Florida
Gainesville, Florida 32611, U.S.A.

ABSTRACT

Thomas Walter, author of *Flora Caroliniana* (1788), left no herbarium. Many of the species he described from the Carolinas and Georgia are without types. Specimens believed to represent 63 of Walter's species are here selected to serve as neotypes or epitypes.

RESUMEN

Thomas Walter, el autor de la *Flora Caroliniana* (1788), no dejó un herbario. Muchas de las especies que describió de las Carolinas y Georgia no tienen tipo. Se seleccionan aquí especimenes que se suponen representan 63 de las especies de Walter, para servir como neotipos o epitipos.

This number of the Thomas Walter Typification Project is a continuation of a report begun previously (Ward 2007c). Here, an additional 63 of Walter's species are addressed, with selection of appropriate neotypes or epitypes.

Although the number of Walter neotypes, as treated in this and previous reports of the Project, have been many, even now not all Walter names have been examined. No effort has been made to typify most of the numerous Walter names that are now remembered only in synonymy. And those names not represented by suitable materials in the herbarium of the present participating institution (GH) will be addressed in a subsequent report.

This report and its immediate predecessor (Ward 2007c) select types for 106 Walter names. Within this number, 101 were selected as neotypes, and 5 as epitypes. The largest proportion, or 98, were of South Carolina collections, 22 of them from Berkeley County; 4 were from Georgia, and 2 each from North Carolina and Florida. A third, or 37, bore a total of 43 annotations confirming the label identifications.

The typifications are presented here in the format used previously (Ward 2007a, 2007b, 2007c), in alphabetical sequence, using the names given them by Thomas Walter.

TYPIFICATIONS

Walter's name: *Daucus divaricatus* Walter (p. 114)
Modern name: **Spermolepis divaricata** (Walt.) Raf.
Common in eastern SC. Identified (from Walter's diagnosis) by Mathias & Constance (1944: 72). Spm. 40-C, a wispy fragment, was labeled "*Daucus*" by Fraser, and annotated as "*divaricatus* Walt." by A. Gray, though one wonders what he saw that was recognizable. *Boufford & Wood 23862, 27 May 1988 - GH*, from Wadmalaw Island, s. of Charleston, Charleston County, South Carolina, is here selected as neotype for *Daucus divaricatus* Walt., basionym of *Spermolepis divaricata* (Walt.) Raf. Known isoneotypes: MO, NY.

Walter's name: *Delphinium carolinianum* Walter (p. 155)
Modern name: **Delphinium carolinianum** Walt.
Almost unknown in SC (a single county), frequent in central GA. *Fraser/Walter 40-B [1787]* - BM, a now-unidentifiable fragment labeled "*Delphinium*" by Walter and "*Carolinianum*" by Fraser, was cited by Warnock (1981: 48), as "Type: South Carolina, within fifty miles of Berkeley Co., T. *Walter s.n.* (BM)." The cited specimen is worthless for identification purposes. *Radford 22407,* 11 May 1957 - *GH* (annot. Michael J.

J. Bot. Res. Inst. Texas 2(1): 475 – 486. 2008

Warnock 1979), from 4.5 mi SE of Clarks Hill, McCormick County, South Carolina, is here selected as EPITYPE for *Delphinium carolinianum* Walt., in support of Warnock's typification. Known ISOEPITYPES: CA, FLAS, GA, NCU, NY.

WALTER'S NAME: *Dianthera ovata* Walter (p. 63)
MODERN NAME: **Justicia ovata** (Walt.) Lindau
Frequent on the SC coastal plain. There is no specimen. *Godfrey & Tryon 545,* 14 Jul 1939 - GH (annot. Martha Meagher 1972), from Andrews, Georgetown County, South Carolina, is here selected as NEOTYPE for *Dianthera ovata* Walt., basionym of *Justicia ovata* (Walt.) Lindau. Known ISONEOTYPES: BH, CA, CAS, MO.

WALTER'S NAME: *Diodia teres* Walter (p. 87)
MODERN NAME: **Diodia teres** Walt.
Common throughout. There is no specimen. *Godfrey & Tryon 1682,* 24 Aug 1939 - GH, from Georgetown, Georgetown County, South Carolina, is here selected as NEOTYPE for *Diodia teres* Walt. Known ISONEOTYPES: NY, US.

WALTER'S NAME: *Doronicum acaule* Walter (p. 205)
MODERN NAME: **Arnica acaulis** (Walt.) BSP.
Common in eastern SC. No specimen. *Hunnewell 12681,* 30 Mar 1933 - GH (annot. Bassett Maguire 1944), from near Goose Creek, Berkeley County, South Carolina, is here selected as NEOTYPE for *Doronicum acaule* Walt., basionym of *Arnica acaulis* (Walt.) BSP.

WALTER'S NAME: *Eriocaulon anceps* Walter (p. 83)
MODERN NAME: **Lachnocaulon anceps** (Walt.) Morong
Common on SC coastal plain. Walter's description was identified by Kral (1966: 319). There is no specimen. *Godfrey & Tryon 1210,* 7 Aug 1939 - GH, from 6 mi S of Columbia, Lexington County, South Carolina, is here selected as NEOTYPE for *Eriocaulon anceps* Walt., basionym of *Lachnocaulon anceps* (Walt.) Morong. Known ISONEOTYPES: NY, US.

WALTER'S NAME: *Ervum erectum* Walter (p. 187)
MODERN NAME: **Galactia erecta** (Walt.) Vail
Frequent in eastern SC. No specimen has been identified. *Godfrey 147,* 10 Sep 1939 - GH, from 5 mi S of Andrews, Georgetown County, South Carolina, is here selected as NEOTYPE for *Ervum erectum* Walt., basionym of *Galactia erecta* (Walt.) Vail. Known ISONEOTYPES: BH, DUKE, F, MO, NY, US.

WALTER'S NAME: *Eryngium integrifolium* Walter (p. 112)
MODERN NAME: **Eryngium integrifolium** Walt.
Frequent on the SC coastal plain. Sp. 42-D was numbered "716" by Fraser, then labeled "*Eryngium nov.*" by Walter, with "*Integrifolium*" added by Fraser. The specimen is of inadequate, scarcely identifiable quality. *Wilbur & Webster 2861,* 31 Aug 1950 - GH, from 6 mi E of Summerville, Berkeley County, South Carolina, is here selected as NEOTYPE for *Eryngium integrifolium* Walt. Known ISONEOTYPES: MICH, NY, US.

WALTER'S NAME: *Erysimum pinnatum* Walter (p. 174)
MODERN NAME: **Descurainia pinnata** (Walt.) Britt.
Infrequent on SC coastal plain, unknown inland. The label of spm. 43-A bears "*Erysimum*" in Walter's hand, and "*Pinnatum*" in Fraser's; it also carries Fraser's 3-digit number. Although Walter saw this specimen, better material would have been available to him in the field. *Godfrey 3515,* 17 Apr 1938 - GH, from Brookgreen Gardens, Georgetown County, South Carolina, is here selected as NEOTYPE for *Erysimum pinnatum* Walt., basionym of *Descurainia pinnata* (Walt.) Britt. Known ISONEOTYPES: US.

Walter's name: *Ethulia uniflora* Walter (p. 195)
Modern name: **Sclerolepis uniflora** (Walt.) BSP.
Frequent in eastern SC. Spm. 15-F appears to be this (even though it atypically bears 2 heads). The label ("*Ethulia Uniflora*") is in Fraser's hand. Since there is no evidence Walter saw or used this specimen, *Ahles 53495,* 25 May 1960 - GH, from 3 mi SW of Moncks Corner, Berkeley County, South Carolina, is here selected as neotype for *Ethulia uniflora* Walt., basionym of *Sclerolepis uniflora* (Walt.) BSP. Known isoneotypes: CA, FLAS, GA, MICH, NCU, NY, US, USCH.

Walter's name: *Eupatorium incarnatum* Walter (p. 200)
Modern name: **Fleischmannia incarnata** (Walt.) King & H. Robins. [= *Eupatorium incarnatum* Walt.]
Rare in SC (but incl. Berkeley Co.). Spm. 46-D was identified as *Eupatorium incarnatum* by Fernald & Schubert (1948: 227), but not called type. The specimen is poor, and bears only the label "*Eupatorium*" in Fraser's hand. Without indication the Fraser specimen was seen or used by Walter, *Ahles 34320,* 18 Sep 1957 - GH, from along Broad River, Cherokee County, South Carolina, is here selected as neotype for *Eupatorium incarnatum* Walt., basionym of *Fleishmannia incarnata* (Walt.) King & Robins. Known isoneotypes: GA, NCU, NY.

Walter's name: *Eupatorium linearifolium* Walter (p. 199)
Modern name: **Eupatorium hyssopifolium** L. [= *E. hyssopifolium* var. *calcaratum* Fern & Schub.]
Frequent throughout. Walter's description ("*foliis linearibus integris subverticillatis...*") exactly matches the linear entire mostly verticillate leaves of *E. hyssopifolium*. Spm. 44-B is the lanceolate serrate mostly opposite-leaved variant of *E. hyssopifolium*, or *E. torreyanum* Short. But Fernald and Schubert (1948: 226–227) mistakenly assumed the specimen to be the type of *Eupatorium linearifolium*, which they treated as specifically distinct from *E. hyssopifolium*. The specimen bears the label "*Eupatorium*" in Walter's hand, but presents no evidence it had been used by him. A specimen that matches Walter's description, *Godfrey & Tryon 1614,* 10 Aug 1939 - GH (annot. Robert K. Godfrey 1973), from 3 mi W of Bonneau, Berkeley County, South Carolina, is here selected as neotype for *Eupatorium linearifolium* Walt. [= *Eupatorium hyssopifolium* L.].

Walter's name: *Festuca octoflora* Walter (p. 81)
Modern name: **Festuca octoflora** Walt. [= *Vulpia octoflora* (Walt.) Rydb.]
Common throughout. There is no specimen. *Boufford 12781,* 13 Apr 1974 - GH, from Columbia, Richland County, South Carolina, is here selected as neotype for *Festuca octoflora* Walt.

Walter's name: *Galega spicata* Walter (p. 188)
Modern name: **Tephrosia spicata** (Walt.) Torr. & A. Gray
Common throughout. Spm. 49-B may be the specimen referred to by Wood (1949: 292) as the type of *Galega spicata* ("GH - photograph of Type in Herb. Walt."). But since Wood cited only the herbarium, not a specific specimen, leaving uncertainty which specimen was intended, unambiguous typification is justified. *Godfrey & Tryon 1310,* 7 Aug 1939 - GH, from 14 mi S of Columbia, Lexington County, South Carolina, is here selected as neotype for *Galega spicata* Walt., basionym of *Tephrosia spicata* (Walt.) Torr. & A. Gray. Known isoneotypes: CA ("1311"), NY, US.

Walter's name: *Hibiscus aculeatus* Walter (p. 177)
Modern name: **Hibiscus aculeatus** Walt.
Common in eastern SC. No specimen. *Wiegand & Manning 1959, 10 Jul 1927* - GH, from 3 mi S of Lake City, Florence County, South Carolina, is here selected as neotype for *Hibiscus aculeatus* Walt. Known isoneotypes: BH.

Walter's name: *Hibiscus coccineus* Walter (p. 177)
Modern name: **Hibiscus coccineus** Walt.
Not presently known in NC, SC, or GA (reported from GA by Small 1933), apparently unknown n. of Duval Co., FL. An old (undated) specimen has been seen from Charleston, SC (GH), perhaps from cultivation. Spm. 58-E is clearly this; it bears Fraser's number "674" (an indication of mid-season collection, thus it could not have been obtained on Fraser's spring trip into southern Georgia). It was labeled "*Hibiscus*" by Walter, with "*Coccineus*" added by Fraser. Though spm. 58-E could be claimed a lectotype, the possibility that Walter may have had seen it near Charleston, his market town, and his failure to note Fraser's specimen as a species of his own making, makes that status unlikely. *Blanchard 173, 14 Jul 1968 - GH*, from Fla. 16, 0.4 mi E of St. Johns River, between Orangedale and Green Cove Springs, St. Johns County, Florida, is here selected as neotype of *Hibiscus coccineus* Walt. Known isoneotypes: CAS.

Walter's name: *Hydrastis caroliniensis* Walter (p. 156)
Modern name: **Trautvetteria caroliniensis** (Walt.) Vail
Nearly absent from SC, but common in western NC; probably a Fraser discovery. Spm. 1-E is of poor quality, and was mislabeled "*Actea racemosa?*" by Walter. Although Walter may have known this species only by way of Fraser's collections, his failure to recognize spm. 1-E as a species he himself had named makes unlikely his having used it in his writing. Thus, rather than designating spm. 1-E as lectotype, *Curtiss 30, Jul [1892?] - GH*, from grassy "balds" of Roan Mtn., Mitchell County, North Carolina, is here selected as neotype for *Hydrastis caroliniensis* Walt., basionym of *Trautvetteria caroliniensis* (Walt.) Vail. Known isoneotypes: BH, F, GA, NY, PH, US.

Walter's name: *Hyoseris biflora* Walter (p. 194)
Modern name: **Krigia biflora** (Walt.) Blake
Absent from SC, frequent in western NC. Identified by Blake (1915: 135). No specimen in the herbarium. *Cronquist 4349, 27 Apr 1947 - GH*, from near Flint River, 4 mi SE of Woodbury, Upson County, Georgia, is here selected as neotype for *Hyoseris biflora* Walt., basionym of *Krigia biflora* (Walt.) Blake. Known isoneotypes: FLAS, GA, MO, NY, US.

Walter's name: *Hypericum denticulatum* Walter (p. 190)
Modern name: **Hypericum denticulatum** Walt.
Common in eastern SC. No specimen. *Wiegand & Manning 2018, 13 Jul 1927 - GH*, from 3 mi S of Bonneau, Berkeley County, South Carolina, is here selected as neotype for *Hypericum denticulatum* Walt. Known isoneotypes: BH.

Walter's name: *Hypericum petiolatum* (p. 191)
Modern name: **Triadenum walteri** (Gmel.) Gleason [= *Hypericum walteri* Gmel.; = *Triadenum petiolatum* (Walt.) Britt.]
Frequent throughout. Not *Hypericum petiolatum* L.; Walter's *Hypericum petiolatum* was a later homonym (1763 vs. 1788) and thus illegitimate. But Gmelin's replacement (1791) was based on Walter's name and description. No specimen has been identified. *Duncan 13239, 20 Sep 1951 - GH*, from 4.2 mi E of Lafayette, Walker County, Georgia, is here selected as neotype for *Hypericum walteri* Gmel. [= *Triadenum walteri* (Gmel.) Gleason]. Known isoneotypes: BH, FLAS, GA, US.

Walter's name: *Ilex decidua* Walter (p. 241)
Modern name: **Ilex decidua** Walt.
Frequent throughout. Spms. 61a-H and 61a-J appear to be this, the first labeled "*Ilex decid*" by Walter, the second "*Ilex Decidua*" by Fraser. Both are of poor quality. *Godfrey & Tryon 652,* 17 Jul 1939 - GH, from the Santee River floodplain, 3 mi NE of Pineville, Berkeley County, South Carolina, is here selected as neotype of *Ilex decidua* Walt. Known isoneotypes: BH, CA, CAS, DUKE, F, MO, NY, PH, US.

WALTER'S NAME: *Ilex myrtifolia* Walter (p. 241)
MODERN NAME: **Ilex myrtifolia** Walt. [= *Ilex cassine* L. var. *myrtifolia* (Walt.) Sarg.]
Common in eastern SC. Spm. 61a-D was labeled "*Ilex Myrtifolia*" by Fraser and has been annotated as "type" (by J.E. Dandy?), but is a small twig of poor quality. Spms. 61a-E, 61a-G, and 61a-I appear to be the same species, and are even poorer. Since spm. 61a-D appears not to have been published as type, *Bozeman 11368,* 27 Aug 1967 - GH (annot. Ross C. Clark 1994), from Francis Marion National Forest, 1.6 mi N of Honey Hill, Berkeley County, South Carolina, is here selected as NEOTYPE of *Ilex myrtifolia* Walt. Known ISONEOTYPES: MICH, NCU, NY.

WALTER'S NAME: *Iris tripetala* Walter (p. 66)
MODERN NAME: **Iris tridentata** Pursh
Frequent on SC coastal plain. Not *Iris tripetala* L.f. (1782). There is no specimen. Though Walter's name is usually treated as a synonym of *Iris tridentata, Leonard & Radford 1599,* 2 Jun 1968 - GH, from Georgetown County, South Carolina, is here selected as NEOTYPE for *Iris tripetala* Walt. Known ISONEOTYPES: CA, FLAS, GA, NCU, NY.

WALTER'S NAME: *Ischaemum secundatum* Walter (p. 249)
MODERN NAME: **Stenotaphrum secundatum** (Walt.) Kuntze
Infrequent in eastern SC. Identified by Hitchcock (1905: 55) from Walter's description. There is no specimen. The species in the Southeast consists of two variants ("demes"), one native, one introduced (Sauer 1972). *Ahles 15602,* 27 Jun 1956 - GH (annot. J.D. Sauer 1971), from roadbank, U.S. 21, Beaufort, Beaufort County, South Carolina, is here selected as NEOTYPE for *Ischaemum secundatum* Walt., basionym of *Stenotaphrum secundatum* (Walt.) Kuntze. Known ISONEOTYPES: GA, NCU, NY.

WALTER'S NAME: *Kalmia hirsuta* Walter (p. 138)
MODERN NAME: **Kalmia hirsuta** Walt.
Rare in SC (5 counties). Spm. 62b-C, a nearly bare twig, was labeled "*Kalmia Hirsuta Nova*" by Fraser. Southall & Hardin (1974) referred to a specimen on page 62 as the "type." Their typification has been corrected (Ward 2007a) to lectotype. The specimen, however, is unidentifiable without the label and serves no useful purpose as a type. *Bell 3956,* 29 Jun 1956 - GH (annot. J.E. Ebinger 1972), from S.C. 631, 1 mi SE of Hampton County line, Jasper County, South Carolina, is here selected as EPITYPE, in support of Southall & Hardin's typification of *Kalmia hirsuta* Walt. (as corrected).

WALTER'S NAME: *Leontodon carolinianum* Walter (p. 192)
MODERN NAME: **Pyrrhopappus carolinianus** (Walt.) DC.
Frequent throughout. This may be spm. 64-F, which was labeled "*Leontodon novum*" by Walter, and "*Carolinianum*" by Fraser. It is very poor. A specimen with cauline leaves, *Wiegand & Manning 3518,* 11 Jul 1927 - GH, from 4 mi S of Kingstree, Williamsburg County, South Carolina, is here selected as NEOTYPE for *Leontodon carolinianum* Walt., basionym of *Pyrrhopappus carolinianus* (Walt.) DC. Known ISONEOTYPES: BH.

WALTER'S NAME: *Lilium Catesbaei* Walter (p. 123)
MODERN NAME: **Lilium catesbaei** Walt.
Infrequent on SC coastal plain, but a striking plant and likely known to Walter. Spm. 64-E is this, although labeled "*Lilium philadelphicum*" by Walter. Since the specimen is of poor quality, and appears not to have been recognized by Walter, *Godfrey & Tryon 1046,* 2 Aug 1939 - GH, from 11 mi N of Georgetown, Georgetown County, South Carolina, is here selected as NEOTYPE for *Lilium catesbaei* Walt. Known ISONEOTYPES: BH, CA, CAS, DUKE, F, MO, NY.

Walter's name: *Linum striatum* Walter (p. 118)
Modern name: **Linum striatum** Walt.
Infrequent throughout. No specimen. *Godfrey & Tryon 637,* 17 Jul 1939 - GH (annot. C. M. Rogers 1960), from Santee Canal, 5 mi W of Pineville, Berkeley County, South Carolina, is here selected as neotype for *Linum striatum* Walt. Known isoneotypes: CA, NY, US.

Walter's name: *Ludwigia arcuata* Walter (p. 89)
Modern name: **Ludwigia arcuata** Walt.
Very rare in SC (3 counties, but one is Charleston, Walter's market town). No specimen appears to be this species. But Peng et al. (2005: 345) cited spm. 66-D as "holotype" of *Ludwigia arcuata*, apparently in gross error! (The cited specimen appears to be *L. pilosa*, and was so labeled by Walter.) With the expectation that the error will be acknowledged and effort undertaken to correct the erroneous typification via conservation, *Radford 11411,* 8 Sep 1967 - GH, from Millettville, Allendale County, South Carolina, is here selected as neotype for *Ludwigia arcuata* Walt. Known isoneotypes: CA, CAS, FLAS, GA, MICH, NCU, NY, USCH.

Walter's name: *Ludwigia glandulosa* Walter (p. 88)
Modern name: **Ludwigia glandulosa** Walt.
Frequent in eastern SC. No specimen has been identified. *Wilbur 74177,* 15 Aug 2001 - GH, from Red Bluff, Horry County, South Carolina, is here selected as neotype for *Ludwigia glandulosa* Walt. Known isoneotypes: DUKE.

Walter's name: *Ludwigia suffruticosa* Walter (p. 90)
Modern name: **Ludwigia suffruticosa** Walt.
Frequent in eastern SC. No specimen has been identified. *Wiegand & Manning 2200,* 10 Jul 1927 - GH (annot. P.A. Munz 1942; C-I Peng 1981), from 6 mi N of Kingstree, Williamsburg County, South Carolina, is here selected as neotype for *Ludwigia suffruticosa* Walt. Known isoneotypes: BH.

Walter's name: *Lycium carolinianum* Walter (p. 84)
Modern name: **Lycium carolinianum** Walt.
There is no specimen. A coastal plant, at times reported for SC, but only on the basis of Walter's listing, and a note in Elliott. Presently unknown in SC; almost unknown in GA (Camden Co., the southeastern corner). Undoubtedly a discovery of Fraser's, but it is difficult to understand how he could have journeyed that far south. Perhaps since his time the range of this cold-sensitive plant has contracted southward. This possibility is supported by Elliott (1816: 1: 200): "I have never seen this plant in its native state, where it is said to be of very humble growth. Found by Mr. Wm. Bartram, in the saline rushy marshes of Carolina." *Curtiss 6543,* 10 Oct 1899 - GH (annot. C.L. Hitchcock 1930), from mouth of St. Johns River, [Duval County], Florida, is here selected as neotype for *Lycium carolinianum* Walt. Known isoneotypes: BH, CA, CAS, DS, G, MO, NY, UC, US. This collection was noted by C.L. Hitchcock (1932: 239) as: "no type designated, but Curtiss's number 6543 is taken as typically representing this species."

Walter's name: *Melanthium Muscaetoxicum* Walter (p. 125)
Modern name: **Zigadenus muscaetoxicum** (Walt.) Regel [= *Amianthium muscaetoxicum* (Walt.) A. Gray]
Frequent throughout. Spm. 58-C was labeled "*Helonias bullata?*" by Walter, in reference to *H. bullata* L., a northern species that reaches NC (two counties) but is unknown in SC. Walter did not include *H. bullata* in his *Flora*. Though he knew *Zigadenus muscaetoxicum*, which he included as "*Melanthium Muscaetoxicum*," he apparently did not recognize the immature plant collected by Fraser. *Weatherby & Griscom 16486,* 1 May 1932 - GH, from Myrtle Beach, Horry County, South Carolina, is here selected as neotype for *Melanthium muscaetoxicum* Walt., basionym of *Zigadenus muscaetoxicum* (Walt.) Regel. Known isoneotypes: NY.

Walter's name: *Melica mutica* Walter (p. 78)
Modern name: **Melica mutica** Walt.
Frequent throughout. There is no specimen. *Griscom 511,* 11 Apr 1932 - GH (annot. W.S. Boyle 1943), from Myrtle Beach, Horry County, South Carolina, is here selected as neotype for *Melica mutica* Walt. Known isoneotypes: BH, CA, CAS, DUKE, F, GA, MICH, MO, NCU, NY, PH.

Walter's name: *Mespilus aestivalis* Walter (p. 148)
Modern name: **Crataegus aestivalis** (Walt.) Torr. & A. Gray
Rare in SC (3 counties, incl. Berkeley). No specimen. *Harbison s.n.,* 15 Mar & 21 May 1916 - GH, from along Combahee River, E of Yemassee, [Colleton Co.], South Carolina, is here selected as neotype for *Nespilus aestivalis* Walt., basionym for *Crataegus aestivalis* (Walt.) Torr. & A. Gray. Known isoneotypes: NCU.

Walter's name: *Nyssa biflora* Walter (p. 253)
Modern name: **Nyssa biflora** Walt. [= *Nyssa sylvatica* Marsh. var. *biflora* (Walt.) Sarg.]
Frequent in eastern SC. Spms. 75-A, 75-B, or 75-C may be this, but are poor. (The first was labeled "*Nyssa*," the second "*Nyssa Multiflora*," both by Fraser, and the third "*Nyssa*" by Walter.) *Little 14304,* 15 Jun 1951 - GH, from Hell Hole Bay, S of Jamestown, Berkeley County, South Carolina, is here selected as neotype for *Nyssa biflora* Walt.

Walter's name: *Obolaria caroliniana* Walter (p. 166)
Modern name: **Bacopa caroliniana** (Walt.) Robins.
Common in eastern SC. Pennell (1920: 243) stated: "Description sufficiently distinctive." Pennell (1946) again recognized Walter's description as this species and used this name, but designated no type. No corresponding specimen is apparent. *Godfrey & Tryon 948,* 26 Jul 1939 - GH (annot. H.S. Wooden 1979), from 1 mi S of Sandinia, Clarendon County, South Carolina, is here selected as neotype for *Obolaria caroliniana* Walt., basionym for *Bacopa caroliniana* (Walt.) Robins. Known isoneotypes: NY, US.

Walter's name: *Paspalum praecox* Walter (p. 75)
Modern name: **Paspalum praecox** Walt.
Hitchcock (1905: 42) noted Walter's name now to be "generally acepted by American botanists." Plants of this name are infrequent on the SC coastal plain. There is no specimen. For stability, *Godfrey & Tryon 84,* 23 Jun 1939 - GH, from Georgetown, Georgetown County, South Carolina, is here selected as neotype for *Paspalum praecox* Walt. Known isoneotypes: BH, CAS, DUKE, MICH, NY, PH, US.

Walter's name: *Pinus glabra* Walter (p. 237)
Modern name: **Pinus glabra** Walt.
Frequent in southeastern SC. Dayton (1952) and Ward (1962) confirmed Walter's description; Dayton identified spms. 83-D and 83-H as this species. Dayton proposed that these two specimens "perhaps should be considered the type material" of *Pinus glabra*, but made no designation. Though spm. 83-H was labeled "*Pinus*" by Walter (and spm. 83-H by Fraser), there is no evidence Walter used it in forming his description. *Palmer 35395,* 16 May 1929 - GH, from Seneca, Oconee County, South Carolina, is here selected as neotype for *Pinus glabra* Walt. Known isoneotypes: MO, NY, US.

Walter's name: *Pinus squarrosa* Walter (p. 237)
Modern name: **Pinus echinata** Mill.
Common throughout. Dayton (1952) and Ward (1962) confirmed Walter's description; Dayton identified spms. 83-I (labeled "*Pinus*" by Walter) and 83-J (unlabeled) as this species. Dayton (1952: 71) suggested, "it is possible that this [spm. 83-I] may be the type of Walter's *P. squarrosa*." However he stopped short of designating the specimen as type. A better specimen, with cones, *Godfrey & Tryon 1453,* 10 Aug 1939

- GH, from 3 mi W of Bonneau, Berkeley County, South Carolina, is here selected as NEOTYPE for *Pinus squarrosa* Walt. (= *Pinus echinata* Mill.). Known ISONEOTYPES: CA, CAS, NY, US.

WALTER'S NAME: *Polygala cymosa* Walter (p. 179)
MODERN NAME: **Polygala cymosa** Walt.
Common in eastern SC. Smith & Ward (1976) referred to a "holotype," but noted "not seen and presumably no longer extant." Spm. 84-B, labeled "*Polygala*" by Fraser, has since been identified as *P. cymosa*. It is of poor quality, consisting solely of an upper inflorescence. In the absence of evidence that spm. 84-B was seen or used by Walter, *Godfrey & Tryon 67,* 24 Jun 1939 - GH (annot. Foard 1959), from 15 mi N of Georgetown, Georgetown County, South Carolina, is here selected as NEOTYPE of *Polygala cymosa* Walt. Known ISONEOTYPES: BH, CA, CAS, DUKE, F, MO, NY, US.

WALTER'S NAME: *Polygala grandiflora* Walter (p. 179)
MODERN NAME: **Polygala grandiflora** Walt.
Frequent in eastern SC. There is no specimen. Rodriguez (2003) stated the "Holotipo" to be "Carolina, *Walter* (BM)," with a symbol indicating the specimen had been lost or destroyed. Since no specimen could be designated, no typification took place. *Batchelder 4905,* 30 Apr 1917 - GH, from Ladies Island, Beaufort, Carteret County, North Carolina, is here selected as NEOTYPE of *Polygala grandiflora* Walt. Known ISONEOTYPES: MO.

WALTER'S NAME: *Polygala polygama* Walter (p. 179)
MODERN NAME: **Polygala polygama** Walt.
Frequent throughout. No specimen has been identified. *Palmer 42407,* 19 May 1934 - GH, from Columbia, Richland County, South Carolina, is here selected as NEOTYPE of *Polygala polygama* Walt.

WALTER'S NAME: *Polygonum hirsutum* Walter (p. 132)
MODERN NAME: **Polygonum hirsutum** Walt.
Rare in SC (4 counties, though one is Charleston, Walter's market town). No specimen has been identified. *Ahles 15868,* 20 Jun 1956 - GH, from Barton, Allendale County, South Carolina, is here selected as NEOTYPE for *Polygonum hirsutum* Walt. Known ISONEOTYPES: NY.

WALTER'S NAME: *Quercus laevis* Walter (p. 234)
MODERN NAME: **Quercus laevis** Walt.
Common in eastern SC. No specimen. *Hill 18860,* 21 Sep 1987 - GH, from Bluefield Road, Lexington County, South Carolina, is here selected as NEOTYPE for *Quercus laevis* Walt. Known ISONEOTYPES: MO, NCU, NY, USCH.

WALTER'S NAME: *Quercus lyrata* Walter (p. 235)
MODERN NAME: **Quercus lyrata** Walt.
Common in eastern SC. No specimen. *Spongberg 17209,* 14 Sep 1982 - GH, from Perrysburg Landing, WNW of Hardeeville, Jasper County, South Carolina, is here selected as NEOTYPE of *Quercus lyrata* Walt.

WALTER'S NAME: *Quercus pumila* Walter (p. 234)
MODERN NAME: **Quercus pumila** Walt. [= *Quercus elliottii* Wilbur]
Common in eastern SC. Spm. 90-E is poor, and though it was seen (and labeled, as "*Quercus pumila*") by Walter, there is no suggestion that it was used by him. *Godfrey & Tryon 1420,* 11 Aug 1939 - GH, from 8 mi S of Moncks Corner, Berkeley County, South Carolina, is here selected as NEOTYPE for *Quercus pumila* Walt. Known ISONEOTYPES: *NY, US*. Wilbur (2002: 138–140) has argued that Walter's description was defective, and that the small shrub should be renamed *Quercus elliottii* Wilbur. In light of the near-certainty that Walter knew his *Quercus pumila* (as seen within stone-throw of his grave - D.B.W. obs., Jun 1990), the new name is superfluous.

WALTER'S NAME: *Rhexia petiolata* Walter (p. 130)
MODERN NAME: **Rhexia petiolata** Walt.
Frequent in eastern SC. James (1956: 216) tentatively designated a specimen, *Fraser/Walter 91-D [1787] - BM*, marked "*Rhexia* 723" as "type" of *Rhexia petiolata* Walt. (The "*Rhexia*" is in Walter's hand, the "723" in Fraser's.) James' typification has been corrected (Ward 2007a) to neotype for *Rhexia petiolata* Walt. James noted, "Positive identification has not been possible because of the fragmentary condition of the specimen..." The specimen (91-D) is a bare stem, quite lacking in identifiable features. *Wiegand & Manning 2126,* 8 Jun 1927 - GH, from 4 mi S of Florence, Florence County, South Carolina, is here selected as EPITYPE, in support of James' typification of *Rhexia petiolata* Walt. (as corrected). Known ISONEOTYPES: BH.

WALTER'S NAME: *Salsola caroliniana* Walter (p. 111)
MODERN NAME: **Salsola kali** L. var. **caroliniana** (Walt.) Nutt.
Infrequent along SC coast. Spm. 93-F was labeled "*Salsola Kali*" by Walter, then the epithet was struck and "*Caroliniana*" added by Fraser. Though only a varietal name is at issue, *Godfrey & Tryon 1571,* 17 Aug 1939 - GH (annot. H.D. Wilson 1981; S. Mosyakin 1994), from South Island, Georgetown County, South Carolina, is here selected as NEOTYPE for *Salsola caroliniana* Walt., basioym of *Salsola kali* L. var. *caroliniana* (Walt.) Nutt. Known ISONEOTYPES: BH, CA, DUKE, MO, NY, PH, US.

WALTER'S NAME: *Silene caroliniana* Walter (p. 142)
MODERN NAME: **Silene caroliniana** Walt.
Frequent throughout SC. Spm. 98-G was labeled "*Silene an virginica?*" by Walter. Wilbur (1970) referred to comments of J.K. Small and C.A. Weatherby—neither of who personally saw the Walter herbarium—to conclude the specimen was unclear as to its subspecies, and that "Walter's description is unmistakable and would take precedence over any specimen in the Walter herbarium." Thus *Weatherby 6114,* 27 Apr 1932 - GH (annot. R.T. Clausen 1938; Bassett Maguire 1941; R.L. Wilbur 1968 & 1996), from outskirts of Columbia, Lexington County, South Carolina, is here selected as NEOTYPE of *Silene caroliniana* Walt. Known ISONEOTYPES: DUKE, NY, PH.

WALTER'S NAME: *Smilax auriculata* Walter (p. 245)
MODERN NAME: **Smilax auriculata** Walt.
Frequent along SC coast. No specimen is present. *Godfrey & Tryon 1169,* 5 Aug 1939 - GH, from Myrtle Beach, Horry County, South Carolina, is here selected as NEOTYPE for *Smilax auriculata* Walt. Known ISONEOTYPES: BH, CA, CAS, DUKE, PH.

WALTER'S NAME: *Smilax glauca* Walter (p. 245)
MODERN NAME: **Smilax glauca** Walt.
Infrequent on SC coastal plain, common inland. No specimen was found in the Fraser/Walter herbarium by Blake (1918). Blake did find a Fraser specimen with "leaves densely puberulent beneath" in the DeCandolle herbarium, Geneva. He noted however, that the Fraser specimen was not "in any sense a type of Walter's *S. glauca*." A specimen with leaves smooth beneath, *Bell 7168,* 12 May 1957 - GH, from Beaver Creek, NNE of Blair, Fairfield County, South Carolina, is here selected as NEOTYPE for *Smilax glauca* Walt.

WALTER'S NAME: *Smilax pumila* Walter (p. 244)
MODERN NAME: **Smilax pumila** Walt.
Frequent in eastern SC. No specimen is present in the herbarium. *Ahles 20939,* 11 Oct 1956 - GH, from county road, 0.4 mi E of U.S. 21, Beaufort County, South Carolina, is here selected as NEOTYPE for *Smilax pumila* Walt. Known ISONEOTYPES: GA.

Walter's name: *Staehelina elegans* Walter (p. 202)
Modern name: **Liatris elegans** (Walt.) Michx.
Common in southeastern SC. Spm. 101-A, a reasonably complete inflorescence, bears the label "*Staehelina*" in Walter's hand; Fraser added "*Elegans*." Since Walter would have known the plant near his home, he need not have used this specimen in forming his description. *Boufford & Shi 30292,* 25 Sep 2000 - GH, from Halfway Creek road, Francis Marion National Forest, WNW of McClellanville, Berkeley County, South Carolina, is here selected as neotype for *Staehelina elegans* Walt., basionym of *Liatris elegans* (Walt.) Michx.

Walter's name: *Syntherisma serotina* Walter (p. 76)
Modern name: **Digitaria serotina** (Walt.) Michx.
Hitchcock (1905: 44) found Walter's diagnoses separating this and the preceding to be unsatisfactory, but made the identification on the basis of these being the only creeping *Digitaria* "found commonly" in the Carolinas. But, far from common, *D. serotina* is very rare in SC (2 counties), suggesting Walter's second species may also have been the abundant and somewhat variable *D. sanguinalis.* There is no specimen. To stabilize the meaning of *D. serotina* (which is well distinguished elsewhere), *Hitchcock 1557,* 15 Aug 1905 - GH, from "open low ground," South Carolina, is here selected as neotype for *Syntherisma serotina* Walt., basionym of *Digitaria serotina* (Walt.) Michx. Known isoneotypes: CA, MO, NY.

Walter's name: *Syntherisma villosa* Walter (p. 77)
Modern name: **Digitaria filiformis** (L.) Koel. var. **villosa** (Walt.) Fern.
Frequent throughout. Hitchcock (1905: 44) accepted spm. 116-C as corresponding to Walter's diagnosis. The specimen is labeled in Walter's hand. But it is poor and unlikely to have been used by Walter in forming his description. *Andersen 1408,* 1897 - GH (annot. M.L. Fernald 1920), from Oconee County, South Carolina, is here selected as neotype for *Syntherisma villosa* Walt., basionym of *Digitaria villosa* (Walt.) Pers.

Walter's name: *Utricularia purpurea* Walter (p. 64)
Modern name: **Utricularia purpurea** Walt.
Infrequent on the SC coastal plain. There is no specimen. Taylor (1989: 689) stated: "lecto. Barnhart 1916;" but Barnhart's action (1916: 62) was a typification of the segregate genus *Vesiculina* Raf., not a typification of the species *U. purpurea. Godfrey & Tryon 1097, 4 Aug 1939 - GH,* from 6 mi NW of McClellanville, Charleston, South Carolina, is here selected as neotype for *Utricularia purpurea* Walt. Known isoneotypes: *BH, CA, CAS, DUKE, F, MO, US.*

Walter's name: *Viburnum obovatum* Walter (p. 116)
Modern name: **Viburnum obovatum** Walt.
Frequent in eastern SC. The only possible specimen (spm. 108-H) is a fragment, bearing only Fraser's label, "*Viburnum.*" *Godfrey & Tryon 8215,* 24 Jul 1939 - GH (annot. Thomas H. Jones 1978), from 10 mi NE of Moncks Corner, Berkeley County, South Carolina, is here selected as neotype for *Viburnum obovatum* Walt. Known isoneotypes: CA, CAS, DUKE, F, MO, NY, PH, US.

Walter's name: *Vicia caroliniana* Walter (p. 182)
Modern name: **Vicia caroliniana** Walt.
Frequent in eastern SC, more common westward. Spm. 106-D appears to be this species. But since Walter labeled it only as "*Vicia nova*," it is unlikely it was used in preparing his description. *Hunnewell 8163,* 23 Mar 1922 - GH (annot. Robert Dirig 1990), from Goose Creek, Berkeley County, South Carolina, is here selected as neotype for *Vicia caroliniana* Walt.

Walter's name: *Vincetoxicum gonocarpos* Walter (p. 104)
Modern name: **Matelea gonocarpa** (Walt.) Shinners
Infrequent in SC, nearly absent from the coastal plain. Thus likely a Fraser discovery. Spm. 109-A, marked "*Vincetoxicum*" by Walter, was identified as *Matelea gonocarpa* by Drapalik (1970: 76, from photo). But it is sterile, which makes it unlikely to have been of use to Walter, who described the plant in detail (incl. flowers and fruits). A specimen of better quality, *Wiegand & Manning 2629,* 16 Jul 1927 - GH (annot. Donald J. Drapalik 1974), from Meggett, Charleston County, South Carolina, is here selected as neotype for *Vincetoxicum gonocarpos* Walt., basionym of *Matelea gonocarpa* (Walt.) Shinners.

Walter's name: *Viola canina* sensu Walter (p. 219) non *Viola canina* Linnaeus, Sp. Pl. 935. 1753; misapplied.
Modern name: **Viola walteri** House
Infrequent throughout. Not *Viola canina* L., nor *V. conspersa* Rchb. When House (1906) realized Walter had misidentified the Carolina plant he assigned it a new name, *V. walteri*, but based the new name on Walter's diagnosis and presumed type. There is no specimen. *Hunnewell 12638*, 30 Mar 1933 - GH (annot. Harvey E. Ballard 1991), from near Goose Creek, Berkeley County, South Carolina, is here selected as neotype for *Viola canina* sensu Walter (basis for *Viola walteri* House).

Walter's name: *Viola villosa* Walter (p. 219)
Modern name: **Viola villosa** Walt.
Frequent throughout. Spms. 108-D and 108-I may be this species. Both bear Walter's hand, but only to "*Viola*" and a descriptive phrase; both are of poor quality. Brainerd (1907) has argued convincingly that Walter's plant was this species (and not *V. hirsutula* Brainerd, found only inland). *Brainerd s.n.*, 25 Mar 1907 - GH (annot. Landon E. McKinney 1986), from Summerville, Dorchester County, South Carolina, is here selected as neotype for *Viola villosa* Walt.

Walter's name: *Waltheria caroliniana* Walter (p. 175)
Modern name: **Piriqueta caroliniana** (Walt.) Urban
Frequent in southeastern SC. No specimen has been identified. *Ahles 18262*, 9 Sep 1956 - GH, from SC 20, 2.7 mi S of jct. with SC 39, Hampton County, South Carolina, is here selected as neotype for *Waltheria caroliniana* Walt., basionym of *Piriqueta caroliniana* (Walt.) Urban. Known isoneotypes: NCU.

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CHROMOSOME NUMBERS FOR SOUTHWESTERN NORTH AMERICAN SPECIES OF *ANTENNARIA* (ASTERACEAE: GNAPHALIEAE)

Jerry G. Chmielewski

Department of Biology
Slippery Rock University
Slippery Rock, Pennsylvania 16057, U.S.A.

ABSTRACT

Chromosome numbers were determined from somatic material for 30 individuals of *Antennaria* Gaertner (Asteraceae: Gnaphalieae), representing four commonly occurring species from southwestern North America. The counts agree with previous reports for the respective species and are presented without comment.

RESUMEN

Se realizaron recuentos cromosomáticos de material somático de 30 individuos de *Antennaria* Gaertner (Asteraceae: Gnaphalieae), que representan a cuatro especies comunes en el suroeste de Norte América. Los recuentos concuerdan con los realizados previamente en las respectivas especies y se presentan sin comentarios.

Chromosome counts here supplement previous counts for North American *Antennaria*. Cultivation of plants and preparation of somatic material for chromosome number determinations followed the procedures of Chinnappa (1986). Voucher specimens remain in my possession and duplicates are deposited in SLRO. I collected all specimens; staminate specimens are marked with an asterisk (*).

ASTERACEAE

Antennaria howellii Greene. $2n = 112$. **COLORADO: Pueblo Co.:** CO 165, Alpine Park NW of Rye, *Ch3190*; between mileposts 23 and 22, *Ch3193*. **Custer Co.:** CO 165, Bigelow Divide, near milepost 8, *Ch3200*.

Antennaria media Greene. $2n = 56$. **COLORADO: San Juan Co.:** US 550, S of Red Mountain Pass, *Ch3173*; Molas Divide, *Ch3177*.

Antennaria parvifolia Nutt. $2n = 84$. **ARIZONA: Coconino Co.:** US 180, vicinity of Forest Road 760, N of Snowbowl, *Ch3154*; N of Fort Valley Ranch Road, approx. milepost 222, *Ch3155*. **Rio Grande Co.:** US 160, E of South Fork, vicinity of South Fork Rest Area, *Ch3183*; $2n = 112$. **ARIZONA: Coconino Co.:** Kaibab Plateau, AZ 67, just S of Jacob Lake, *Ch3157*. **COLORADO: San Juan Co.:** US 550, Red Mountain Pass at Red Mountain Creek, *Ch3168* (white form), *Ch3169* (red form); alpine meadow S of Red Mountain Pass, *Ch3174* (white form), *Ch3175* (red form); Molas Divide, *Ch3176* (white form), *Ch3178* (pink form). **Mineral Co.:** US 160, Wolf Creek Pass, *Ch3181*, *Ch3182**. **Custer Co.:** CO 165, NW of San Isabel, NW of Beulah Road, *Ch3194* (red form), *Ch3195* (white form); Bigelow Divide, vicinity of milepost 8, *Ch3197**, *Ch3198*.

Antennaria rosea Greene. $2n = 56$. **COLORADO: Coconino Co.:** Kaibab Plateau, US 67, S of Jacob Lake, vicinity of Kaibab Lodge, *Ch3160* (red form), *Ch3161* (white form); S of Kaibab Lodge, *Ch3163*. **San Juan Co.:** US 550, Red Mountain Pass, Red Mountain Creek, *Ch3170*; S of Red Mountain Pass, *Ch3172*; Molas Divide, *Ch3179*. **Pueblo Co.:** CO 165, between mileposts 22 and 23, *Ch3192*. **Custer Co.:** CO 165, NW of San Isabel, NW of Beulah Road, *Ch3196*; Bigelow Divide, vicinity of milepost 8, *Ch3199*.

ACKNOWLEDGMENTS

I thank the Department of Biology, Slippery Rock University for their partial financial support of fieldwork. John L. Strother and Dale E. Johnson provided helpful review comments.

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CHROMOSOME NUMBER OF *THEVETIA AHOUAI* (APOCYNACEAE: RAUVOLFOIDAE: PLUMERIEAE) WITH DISCUSSION ON THE GENERIC BOUNDARIES OF *THEVETIA*

Justin K. Williams and Julia K. Stutzman[1]

Department of Biological Sciences
Sam Houston State University
Huntsville, Texas 77341-2116, U.S.A.

ABSTRACT

The mitotic chromosome count ($2n = 20$) for *Thevetia ahouai* is the first reported chromosome count for *Thevetia* sect. *Ahouai*. The count together with a previous count in *Thevetia* sect. *Thevetia* (also $2n = 20$) provides an additional synapomorphy that further supports the monophyly of *Thevetia* as traditionally recognized. A discussion on the proposal to recognize *Thevetia* sect. *Thevetia* as the genus *Cascabela* is provided.

Key Words: *Thevetia*, Apocynaceae, chromosome number, *Cascabela*, *Cerbera*, Plumerieae

RESUMEN

El recuento cromosomático mitótico ($2n = 20$) de *Thevetia ahouai* es el primero para *Thevetia* sect. *Ahouai*. Este recuento junto con otro previo en *Thevetia* sect. *Thevetia* (también $2n = 20$) aporta una sinapomorfía adicional que apoya la monofilia de *Thevetia* como se ha reconocido tradicionalmente. Se aporta una discusión de la propuesta de reconocer *Thevetia* sect. *Thevetia* como el género *Cascabela*.

Thevetia L. belongs to the Apocynaceae subfamily Rauvolfioideae tribe Plumerieae and comprises eight species of shrubs occurring from Central Mexico to northern South America (Gensel 1969; Williams 1996; Allorge 1998; Endress et al. 2007). According to various specialists in the Apocynaceae, the generic boundaries of *Thevetia* vary. In the concept of *Thevetia* sensu K. Schum. (Schumann 1895; Gensel 1969; Williams 1996; Allorge 1998; Alvarado-Cardenas 2004), eight species are sub-divided between two sections: sect. *Ahouai* K. Schum. with three species—*T. ahouai* (L.) A. DC., *T. amazonica* Ducke, and *T. bicornuta* Mull. Arg.—and sect. *Thevetia* K. Schum. with five species—*T. gaumeri* Hemsl., *T. ovata* (Cav.) A. DC., *T. peruviana* (Pers.) K. Schum., *T. pinifolia* (Standl. & Steyerm.) J.K. Williams, and *T. thevetiodes* (H.B.K.) K. Schum. In the concept of *Thevetia* sensu Lippold (Lippold 1980; Alvarado-Cardenas & Ochoterena 2007) the three species of sect. *Ahouai* are retained in *Thevetia*; the other five species of sect. *Thevetia* are segregated into the genus *Cascablea* Raf. Although Lippold (1980) and Alvarado-Cardenas and Ochoterena (2007) segregate *Thevetia* sensu K. Schum. into the two genera *Thevetia* and *Cascablea*, at no point do they argue against the genera's "close morphological relationship" (Alvarado-Cardenas & Ochoterena 2007). In fact, a recent morphological cladistic analysis (Fig. 1, Alvarado-Cardenas & Ochoterena 2007) nests all eight species of *Thevetia* sensu K. Schum. in a clade supported by six synapomorphies. In short, *Thevetia* sensu K. Schum. is clearly shown to be monophyletic. Nevertheless, Alvarado-Cardenas and Ochoterena (2007) argue for its paraphyly and choose instead to recognize the two sub-clades of the clade (Fig. 1) as distinct genera: *Thevetia* and *Cascabela*.

Chromosome numbers have proven useful in resolving generic relationships in the Apocynaceae (Van der Laan & Arends 1985; Williams 2007). To date, 73 of the 179 genera of the Apocynaceae s.str. (subfamilies Rauvolfioideae and Apocynoidoideae) have been counted (Van der Laan & Arends 1985; Goldblatt & Johnson 2003; Williams 2007). Although previous chromosome counts for sect. *Thevetia* (*T. peruviana*; $2n = 20$) exist, none have been reported for sect. *Ahouai*. The present paper provides the first reported chromosome count for a species of sect. *Ahouai* and discusses the utility of chromosome numbers in interpreting the systematic relationship of *Thevetia* and *Cascabela*.

[1]Current Address: Bridgewater College, Box 1568, Bridgewater, Virginia 22812, U.S.A.

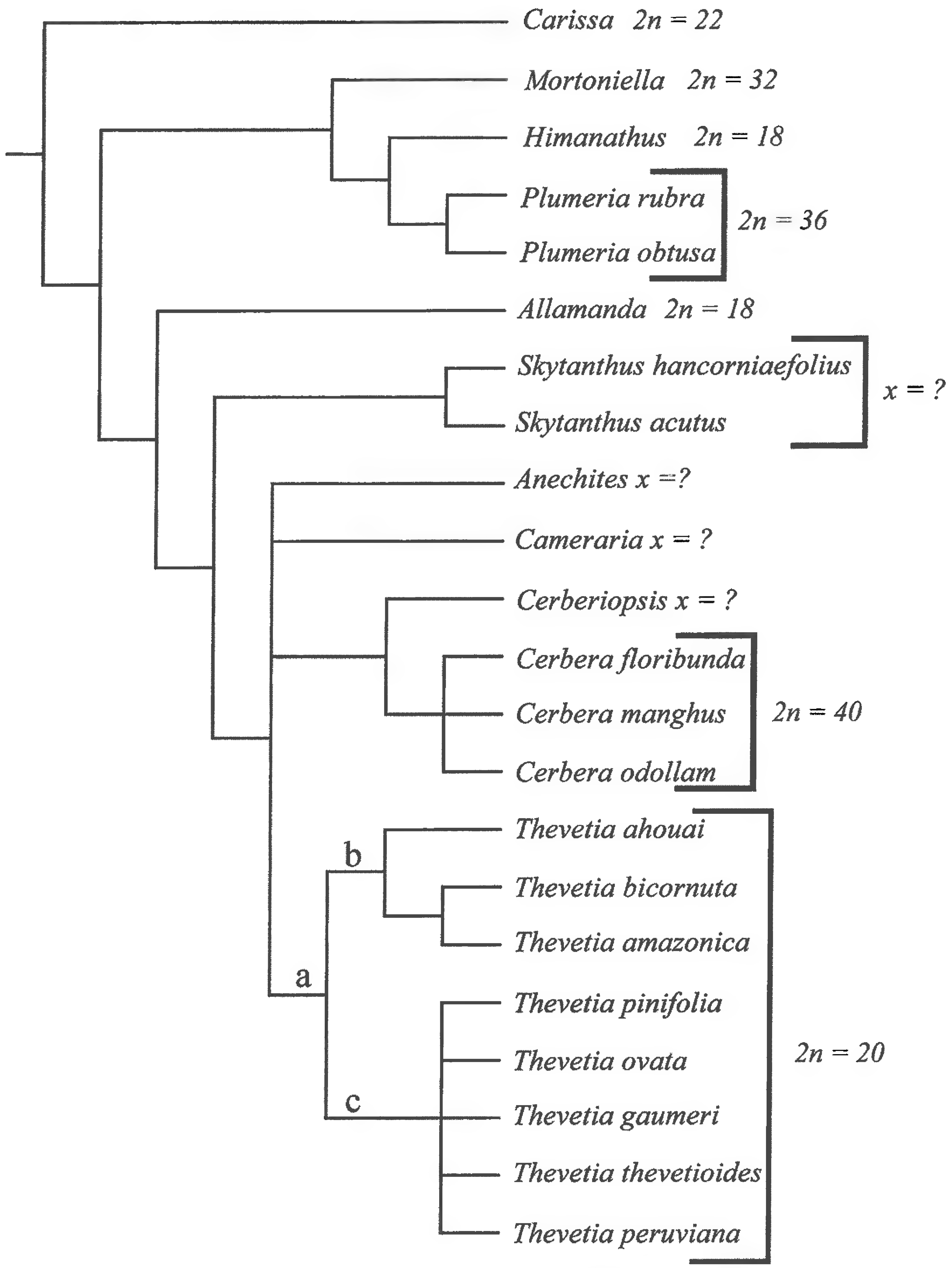

FIG. 1. Morphologically constructed dendogram of "*Plumerieae*" clade (from Alvarado-Cardenas & Ochoterena 2007). a = *Thevetia* sensu K. Schum. and/or "*Cascabela-Thevetia*" clade of Alvarado-Cardenas and Ochoterena 2007. This clade is supported by seven synapomorphies. b = *Thevetia* sect. *Ahouai* and/or *Thevetia* sensu Lippold. This clade is supported by two synapomorphies. c = *Thevetia* sect. *Thevetia* and/or *Cascablea* Lippold. This clade is supported by four synapomorphies.

MATERIALS AND METHODS

Roots tips and voucher specimens were collected from a greenhouse specimen of *Thevetia ahouai* housed at the greenhouse of the Department of Biological Sciences, Sam Houston State University (Table 1). The root tips were fixed and analyzed for chromosome number using standard procedures (Raffauf 1964; Van der Laan & Arends 1985). A voucher specimen of the greenhouse plant was made and is preserved in the Warner Herbarium (SHST).

RESULTS

The format used for reporting chromosome numbers in this article follows that established by Strother and Nesom (1997). A mitotic chromosome number of $2n = 20$ was recorded for *Thevetia ahouai*. Van der Laan and Arends (1985) reported chromosome lengths in the Apocynaceae to be between 0.5–4.0 µm, with the average chromosome length between 1–2 µm. The length of the chromosomes in *T. ahouai* varied between 1–3 µm, consistent with most other chromosomes in the Apocynaceae. The base chromosome number ($x = 10$) for *Thevetia ahouai* is consistent with previous reports of $x = 10$ for *Thevetia* (*T. peruviana* $2n = 20$; Gadella 1977; Ugborogho 1983; Van der Laan & Arends 1985; Santhosh & Omanakumari 1997).

DISCUSSION

Van der Laan and Arends (1985) postulated a base chromosome number of $x = 11$ for the Apocynaceae s. str. based on its prevalence in the family and on the observation that many of the plesiomorphic taxa possess a base number of $x = 11$. A base chromosome number of $x = 10$ is found in four genera representing three of the 11 tribes recognized in the Rauvolfioideae (Endress et al. 2007): Hunterieae (*Gonioma* E. Mey.), Plumerieae (*Cerbera* L., *Thevetia*), and Vinceae (*Ochrosia* Juss.). Based on tribal circumscription (Endress et al. 2007) along with molecular evidence (Simões et al. 2007), $x = 10$ is reconstructed as having evolved independently at least three times in the Rauvolfioideae.

A cursory review of chromosome counts for the Apocynaceae (Van der Laan & Arends 1985; Goldblatt & Johnson 2003) reveals that at present the only chromosome counts for genera in the Plumerieae, and thus relatives to *Thevetia* ($2n = 20$), are for *Allamanda* L. ($n = 9$; $2n = 18$), *Cerbera* ($2n = 40$), *Himatanthus* Willd. ex Schult. ($2n = 18$), *Mortoniella* Woodson ($2n = 32$), and *Plumeria* L. ($2n = 36$). At present there are no chromosome counts for the remaining four genera in the Plumerieae: *Anechites* Griseb., *Cameraria* L., *Cerberiopsis* Vieill. ex Pancher & Sébert, and *Skytanthus* Meyen., and it is suggested here that effort be made to obtain count of these taxa. Figures 1 and 2 present cladograms of the Plumerieae constructed from morphological (Alvarado-Cardenas & Ochoterena 2007) and molecular evidence (Simões et al. 2007), respectively. Diploid counts for the respective genera included in the phylogenies are presented for both Figures 1 and 2.

Alvarado-Cardenas and Ochoterena (2007) presented six synapomorphies that described the *Thevetia* sensu K. Schum. clade (Fig. 1, branch a). The diploid count of $2n = 20$ presented here adds a seventh synapomorphy. When interpreting their data Alvarado-Cardenas and Ochoterena (2007) state that "(t)here is still no consensus regarding the question of whether one should recognize one genus with two (sections) or two distinct genera (Lippold 1980), given that *Cascabela* and *Thevetia* are sister taxa." We would argue that the consensus in evolutionary systematics is to assign generic boundaries that reflect both monophyly and shared ancestry. The decision to divide a well supported clade into two separate genera may support monophyly; however, it excludes shared ancestry. Without prior knowledge, most botanists would be unaware that *Thevetia* and *Cascabela* are sister taxa that share seven synapomorphies. Instead, an evolutionarily more meaningful interpretation of the clade would be that *Thevetia* sensu K. Schum. is monophyletic and support is provided for the recognition of two sections as defined by Schumann (1895). In order to maintain systematic consistency as pertains to current trends in phylogenetic nomenclature we recognize *Thevetia* sensu K. Schum. and regard *Cascabela* and all taxa pertaining to the genus as synonyms of *Thevetia*.

TABLE 1. Voucher specimen for the chromosome number of *Thevetia ahouai*.

Taxon	Voucher specimen	Chromosome number (2n)
Thevetia ahouai	TEXAS: Sam Houston State University Department of Biological Sciences Greenhouse specimen, 22 Jan 2008 *Williams 2008-1* (SHST).	20

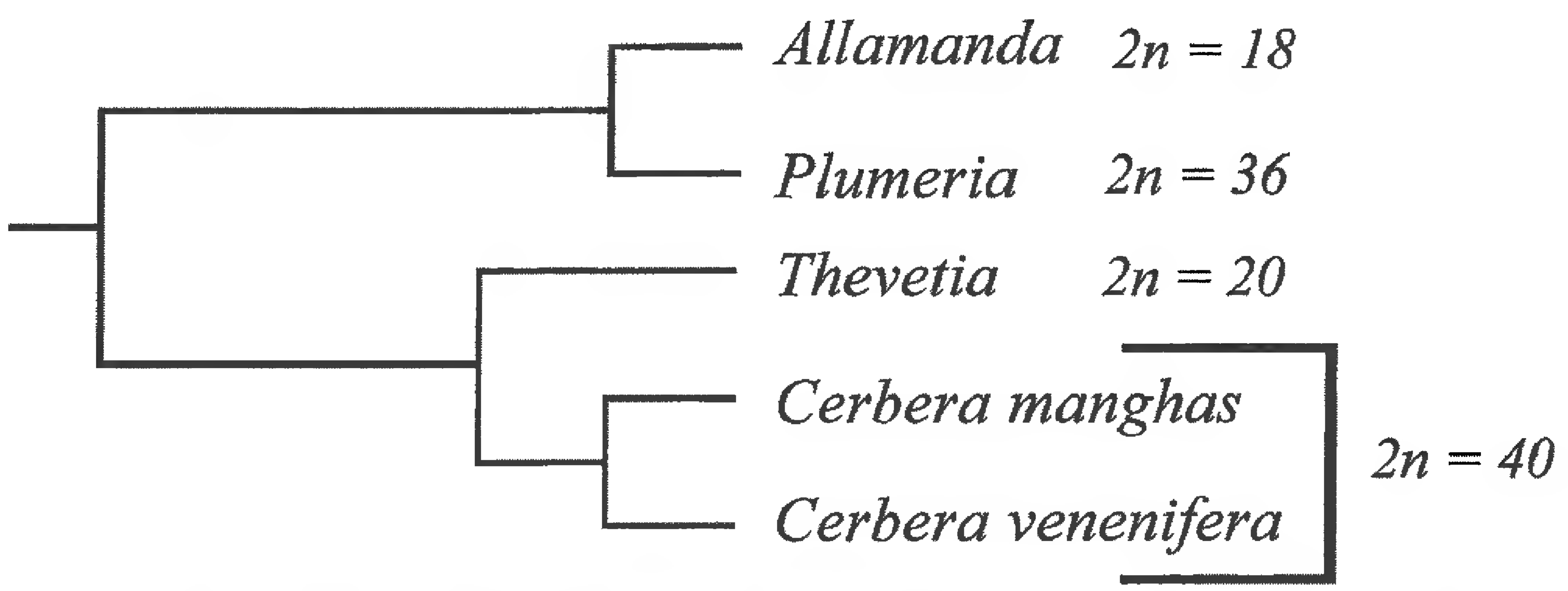

FIG. 2. Molecularly constructed dendogram of "Plumerieae" clade (from Simóes 2007).

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BOOK NOTICES

THE FLORA OF CHINA EDITORIAL COMMITTEE. 2007. **Flora of China, Vol. 12. Hippocastanaceae through Theaceae.** (ISBN Vol. 12: 978-1-930723-64-1, hbk.). Science Press (Beijing) and Missouri Botanical Garden Press (St. Louis), P.O. Box 299, St. Louis, Missouri 63166-0299, U.S.A. (**Orders:** www.mbgpress.org, mbgpress@mobot.org, 1-877-271-1930). $125.00, 534 pp., 8 3/4" × 11 1/4".

From the publishers.—"Eighteen plant families are described in this volume. Among these, Hippocastanaceae comprises the horse chestnuts and buckeyes; Sapindaceae, the soapberry family, includes the fruits lychee and longan, and species valued for their wood; Balsaminaceae, the balsam family, mainly comprises *Impatiens*; Rhamnaceae includes *Rhamnus*, once used for making charcoal for gun-powder, and ornamental plants that contain yellow and green dyes; Vitaceae contains the grapes and numerous other vines; Tiliaceae includes the basswoods, lindens, or limes; Malvaceae contains *Hibiscus*, cotton, and okra; Bombacaceae includes kapok; Sterculiaceae, the source of chocolate, also yields timber; Actinidiaceae includes the edible kiwifruit; and Theaceae includes many ornamental species of *Camellia*, as well as C. *sinensis*, the source of tea."

Editors Wu Zhengyi, Peter H. Raven, and Hong Deyuan state, "[This] is the 14th of a 25-volume work. It includes 18 families, 125 genera, and 1275 species, among which five genera and 767 species (60%) are endemic to China, and eight genera and 29 species (2.3%) are introduced to China." The families covered are (in alphabetical order): Actinidiaceae, Balsaminaceae, Bombacaceae, Dilleniaceae, Elaeocarpaceae, Hippocastanaceae, Leeaceae, Malvaceae, Ochnaceae, Pentaphylacaceae, Rhamnaceae, Sabiaceae, Sapindaceae, Sladeniaceae, Sterculiaceae, Theaceae, Tiliaceae, and Vitaceae. Also included in the text: Preface, Introduction, Acknowledgments, List of Nomenclatural Novelties, Index to Chinese Names, Index to Pinyin Names, Index to Scientific Names, and an Index to Families. A large map of China and its 35 Administrative Divisions is printed on both the inside front cover/front endpaper and the inside back cover/back endpaper.

THE FLORA OF CHINA EDITORIAL COMMITTEE. 2007. **Flora of China Illustrations, Vol. 22. Poaceae.** (ISBN Vol. 22 illustrations: 978-1-930723-61-0, hbk.). Science Press (Beijing) and Missouri Botanical Garden Press (St. Louis), P.O. Box 299, St. Louis, Missouri 63166-0299, U.S.A. (**Orders:** www.mbgpress.org, mbgpress@mobot.org, 1-877-271-1930). $125.00, 937 pp., 8 3/4" × 11 1/4".

From the publishers.—"Volume 22 of the illustrations series is devoted to one plant family of enormous significance, namely, the grasses (Poaceae or Graminae). The Poaceae range from the bamboos within the tribe Bambuseae to the widely cultivated rice, wheat, barley, maize or corn (*Oryza, Triticum, Hordeum*, and *Zea*), as well as many grasses used for animal forage, all plants of unparalleled importance to human life. A large proportion of the species of grasses depicted here, including many woody bamboos, occur naturally only in China."

Editors Wu Zhengyi, Peter H. Raven, and Hong Deyuan state, "This publication is the 12th in a series of 24 volumes of *Flora of China Illustrations*. It accompanies *Flora of China* (FOC) Volume 22, which was published in 2006 and treated 226 genera with 1795 species in the Poaceae. This volume of illustrations includes 904 plates representing a total of 1271 species, 24 subspecies, and 50 varieties in 226 genera of Poaceae." Also included in the text: Preface, Acknowledgments, Index to Chinese Names, Index to Pinyin Names, Index to Scientific Names, Index to Families in the *Flora of China* and the *Flora Reipublicae Popularis Sinicae*, and Published Volumes of the *Flora of China* and the *Flora of China Illustrations*. A large map of China and its 35 Administrative Divisions is printed on both the inside front cover/front endpaper and the inside back cover/back endpaper.

J. Bot. Res. Inst. Texas 2(1): 494. 2008

ANATOMÍA FOLIAR DE ALGUNAS GRAMÍNEAS ALPINAS Y SUBALPINAS DEL EJE VOLCÁNICO TRANSVERSAL, MÉXICO

Maricela Gómez-Sánchez[1] and Kathia Georgina Téllez-Pimienta

Universidad Autónoma de Querétaro
Facultad de Ciencias Naturales, Licenciatura en Biología
Ave. de las Ciencias s/n, 76230 Juriquilla
Querétaro, MÉXICO
gomezs@uaq.mx

RESUMEN

Las prominencias topográficas más altas del Eje Volcánico Transversal albergan pastizales alpinos y subalpinos cuya extensión es reducida y sus hábitats son frágiles. Se estudió la anatomía foliar de 21 especies de gramíneas que habitan estos pastizales, de las cuales 13 son alpinas y ocho subalpinas. Se identificaron dos tipos anatómicos, Pooide y Cloridoide y las vías fotosintéticas C-3 y C-4. Se determinaron nueve caracteres diagnósticos en la epidermis abaxial y 17 en la estructura interna de la lámina foliar. Existen diferencias anatómicas importantes entre las especies de los pastizales alpinos y los subalpinos. A mayor altitud, mayor es el estrés ambiental que enfrentan las especies. Así, en la lámina foliar aumenta el desarrollo de fibras, el tamaño de las células buliformes es mayor, las células incoloras son conspicuas, el clorénquima se reduce, los aguijones aumentan en tamaño y grosor y los estomas se reducen en número. El patrón anatómico de las especies muestra relación estrecha con las condiciones ambientales donde habitan.y es similar al de las especies de zonas desérticas.

ABSTRACT

The highest elevations in the Transmexican Volcanic Belt contain alpine and subalpine grasslands with a reduced extension and their habitats are fragile. The leaf blade anatomy of twenty-one species of grasses that grow in these grasslands was studied. Thirteen species are alpine and eight subalpine. Two anatomical types, Pooid and Cloridoid, and the C-3 and C-4 metabolic pathways were identified. Nine diagnostic characters in the abaxial epidermis and seventeen in the internal structure of the leaf blade were determined. There are important anatomical differences between the species that grow in the alpine grasslands and those from the subalpine. With increasing altitude, there is greater environmental stress for these prairie species. Thus, with increasing altitude the presence of fiber in the leaf blade and the size of the bulliform cells increase along with increases in the size and thickness of the prickles, the colorless cells are conspicuous. In contrast, the chlorenchyma and the stomata number are reduced with altitude. The anatomical pattern of the species shows a close correspondence with the environmental conditions where they grow and it is similar to the species of desert zones.

INTRODUCCIÓN

El Eje Volcánico Transversal es un sistema montañoso que cruza transversalmente México, en su mayor parte entre los paralelos 19° y 20° N. Esta área se sitúa a lo largo de unos 950 km desde la región del Volcán Ceboruco al poniente hasta el Pico de Orizaba al Oriente (Rzedowski 1978). En México, el Eje Volcánico Transversal incluye las prominencias topográficas de mayor altitud que, en sus partes altas albergan manchones de vegetación alpina y subalpina y el área total ocupada por esta vegetación es reducida y está sujeta a cambios ecológicos.

Entre 3500 y 4500 m de altitud se observan comunidades de gramíneas amacolladas, denominadas pastizales o zacatonales alpinos y subalpinos. Los pastizales alpinos se localizan por encima del límite de la vegetación arbórea. El límite superior de este pastizal se sitúa alrededor de 4300 m de altitud, aunque algunas especies de plantas crecen más allá de 4500 m. Los pastizales subalpinos se ubican en claros situados en medio de bosques de *Pinus* L., *Quercus* L. y *Abies* Mill. y la cota aproximada de 4000 m señala la altitud máxima que alcanza el bosque (Rzedowski 1975 y 1978; McDonald 1998).

Las regiones alpinas de México representan uno de los centros más ricos, por unidad de área, de especies endémicas estrictas, muchas de las cuales fueron conocidas para la ciencia hace apenas unos años y, salvo sus distribuciones, no existe conocimiento adicional de estas especies raras. Los hábitats de estas regiones

[1]**Autor para correspondencia**

son los más frágiles dada la corta duración de la estación de crecimiento y la lentitud de los procesos de regeneración que siguen a la perturbación (McDonald 1998).

Los pastizales alpino y subalpino, en forma natural, están condicionados por ciertos factores como temperaturas bajas, disponibilidad de agua, intensidad y duración de luz solar y nutrientes, entre otros. De manera artificial, están condicionados por la tala inmoderada y los incendios, estos últimos usados para provocar el brote de retoños que sirven de alimento para el ganado. La vegetación alpina-subalpina del Eje Volcánico Transversal es única en su tipo y de alto interés biológico, muestra una composición florística notoriamente distinta a la de otras regiones alpinas del país (McDonald 1998) y, es de esperarse que, las especies de estos ambientes posean rasgos anatómicos distintivos y propios de su hábitat.

Los estudios en gramíneas alpinas y subalpinas son pocos y en su mayoría han tenido, principalmente, un enfoque taxonómico donde la anatomía se considera parcialmente. Así, se han abordado revisiones taxonómicas y descripciones de nuevas especies de los géneros *Festuca* L., *Sporobolus* R. Br., *Triniochloa* Hitchc., *Trisetum* Pers., *Muhlenbergia* Schreb., entre otros (González-Ledesma 1991; González y Koch 1994; González-Ledesma et al. 1995, 1998; Hernández y Engleman 1995; Peterson y Herrera-Arrieta 2001; Reyes 2004; Cruz Díaz 2005). Algunos estudios que detallan la anatomía foliar han permitido separar géneros (Valdés-Reyna y Hatch 1995) como *Erioneuron* Nash y *Dasyochloa* Willd. ex Rydb., establecer grupos y subgrupos de las especies mexicanas de *Eragrostis* Wolf (Gómez-Sánchez y Koch 1998), proponer la separación de *Swallenia alexandrae* (Swallen) Soderstr. & H.F. Decker de la subtribu Monanthochloinae Pilg. ex Potzal (Gómez-Sánchez et al. 2001), delimitar algunas especies de *Trisetum* (Hernández y Engleman 1995) y de *Muhlenbergia* (Peterson y Herrera-Arrieta 2001), entre otros.

Este estudio describe y analiza la anatomía de la lámina foliar de algunas gramíneas que habitan en zonas alpinas y subalpinas provenientes de los principales picos montañosos del Eje Volcánico Transversal, en México. Asimismo, los patrones de los gradientes ecológico y geográfico se comparan con las características anatómicofoliares de los diferentes taxa.

MATERIALES Y MÉTODOS

Muestras de especímenes de 21 especies se obtuvieron de los Herbarios CHAPA, ENCB, IEB y QMEX, acrónimos según Holmgren et al. (1990). De cada especie, se estudiaron 1–16 especímenes según la disponibilidad de material. Hojas basales maduras se rehidrataron con agua caliente durante 1–5 minutos. De la parte media de la lámina foliar se hicieron cortes transversales a mano libre con navaja de afeitar para observar la estructura interna. Los cortes se trataron con hipoclorito de sodio al 6% (cloro de uso doméstico) para aclarar y suavizar los tejidos y posteriormente se lavaron con agua corriente. La epidermis abaxial se aisló mediante la técnica de raspado directo y las muestras permanentes se montaron con jalea glicerinada, sin tinción (Gómez-Sánchez y Koch 1998). La epidermis adaxial no se aisló debido a la presencia de surcos fuertemente profundos.

Los caracteres y estados de carácter se seleccionaron por observación directa al microscopio para definir diferencias anatómicas entre especies. Mediante observación se hizo una comparación de los patrones anatómicos entre especies y éstos se compararon con el hábitat. La anatomía foliar se definió con la terminología y descripción de acuerdo a Ellis (1976, 1979) con algunas modificaciones según Gómez-Sánchez y Koch (1998). Las figuras de la anatomía foliar de las especies se elaboraron con ayuda de un microproyector o por observación directa al microscopio. En el caso de la epidermis, están orientadas de tal manera que el eje longitudinal de la lámina foliar aparece en posición horizontal en la ilustración y el ápice de la lámina se ubica a la derecha.

RESULTADOS Y DISCUSIÓN

La anatomía foliar se estudió en 21 especies de gramíneas, seleccionadas por su presencia destacada en los principales picos montañosos del Eje Volcánico Transversal, de las cuales 13 son alpinas y ocho subalpinas (Cuadro 1). La lámina foliar mostró 17 caracteres diferenciales en la estructura interna y nueve en la epidermis

Cuadro 1. Especies estudiadas y ambiente en que habitan.

Especie	Ambiente
Agrostis bourgeaei	Subalpina
A. subpatens	Subalpina
A. tolucensis	Subalpina
Bromus anomalus	Alpina
B. exaltatus	Alpina
Calamagrostis orizabae	Alpina
C. tolucensis	Alpina
Deschampsia liebmanniana	Alpina
Dissanthelium californicum	Subalpina
Festuca hephaestophila	Alpina
F. livida	Subalpina
F. rosei	Alpina
F. tolucensis	Subalpina
Muhlenbergia nigra	Alpina
M. orophila	Alpina
M. quadridentata	Alpina
Peyritschia koelerioides	Alpina
Phleum alpinum	Subalpina
Poa annua	Subalpina
P. orizabensis	Alpina
Triniochloa stipoides	Alpina

abaxial. Con base en la anatomía foliar se identificaron los tipos anatómicos Pooide y Cloridoide. Las especies se arreglaron en dos grupos: Alpino y Subalpino. En el grupo Alpino se identificaron los dos tipos anatómicos, que corresponden a las rutas metabólicas C_3 y C_4. El grupo Subalpino posee especies con tipo aatómico Pooide y metabolismo C_3 (Brown 1958; Ellis 1977).

Las plantas C_3 tienen anatomía no-Kranz y las plantas C_4 tienen anatomía Kranz o de corona (Brown 1977; Ellis 1977). Las especies no-Kranz (C_3) fijan el CO_2 fotosintético mediante la enzima ribulosa 1,5-difosfato carboxilasa y el primer producto es el ácido 3-fosfoglicérico (3-PGA), proceso que sucede en las células clorenquimatosas del mesófilo (Brown 1975 y 1977, Ellis 1977, Gould y Shaw 1983). Anatómicamente estas plantas muestran una vaina interna de paredes gruesas que rodea todos los haces vasculares, o por lo menos los primarios. Al exterior de esta vaina se sitúa otra vaina parenquimatosa que carece de cloroplastos o tiene pocos y de menor tamaño que los cloroplastos del mesófilo. El mesófilo está dispuesto irregularmente (Ellis 1977). Las especies Kranz (C_4) fijan el CO_2, durante las horas de luz, en las células del mesófilo mediante la enzima fosfoenolpiruvato carboxilasa y el primer producto de la fotosíntesis es el ácido oxalacético, ácido málico o ácido aspártico. Estos productos son transferidos a las células de la vaina Kranz donde sucede la descarboxilación y luego la fijación (Brown 1975 y 1977; Ellis 1977; Hattersley y Watson 1976). La anatomía de estas plantas se distingue por poseer una o dos vainas pero, siempre muestran una vaina parenquimatosa (Kranz) alrededor de los haces vasculares separándolos de las predominantes células del mesófilo. Esta vaina tiene sus células grandes y con paredes más gruesas y tienen cloroplastos en mayor cantidad y tamaño que aquellos del mesófilo. El mesófilo es regular y se dispone radialmente alrededor de los haces vasculares (Ellis 1977; Johnson y Brown 1973) y con frecuencia es atravesado por columnas de células incoloras.

Anatomía foliar de Gramíneas Alpinas.—La mayoría de las especies alpinas habitan principalmente por encima de 3500–4500 m de altitud, aunque llegan a crecer en zonas boscosas y en niveles altitudinales inferiores. Estas plantas son herbáceas, perennes, rizomatosas, desarrollan macollas robustas y fuertes y alcanzan de 30–70 cm de altura. Su presencia es notoria en claros de bosques de *Pinus*, en lugares perturbados, a la orilla de caminos y en pastizales alpinos. Este grupo de especies posee rasgos anatómicos en la lámina foliar que lo protegen contra las adversidades del clima propias de los pastizales alpinos o zacatonales,

donde la insolación es alta, la disponibilidad de agua es baja, las sequías y temperaturas son extremas, ocasionalmente hay heladas y los vientos son fuertes. En estas zonas, al igual que en las áreas secas o desérticas, ocurre el fenómeno llamado "verano de día, invierno de noche", ya que durante las horas de insolación se alcanzan temperaturas bastante altas y, al llegar la noche, la temperatura desciende tanto que generalmente el suelo se congela y las plantas no pueden disponer de agua. Esto permite que las plantas muestren rasgos morfológicos que también son propios de aquellas que crecen en ambientes secos y desérticos (Smith y Young 1987). En las zonas subalpinas es común encontrar representantes arbóreos de los géneros *Juniperus*, *Pinus* y *Abies* (Starker 1950) por lo que en estas áreas los vientos no son tan fuertes. A mayor altitud, más desarrollados son los rasgos anatómicos que proporcionan protección contra la evapotranspiración, los daños mecánicos y la insolación, tales como los estomas protegidos, desarrollo de aguijones grandes, micro y macropelos, desarrollo conspicuo de fibras y dispuestas en trabas y células buliformes en abanico y grandes que intervienen en la involución de la lámina, entre otras.

Las especies alpinas exhiben un patrón anatómico distintivo. La lámina foliar muestra cuerpos de sílice y ganchos numerosos, las púas son largas y de base ancha sobre el margen, el esclerénquima está dispuesto en trabas o en hebras de tres células de ancho y 6–8 células de alto, el clorénquima es reducido y las células buliformes son grandes que se disponen en formas diversas, y las células incoloras son conspicuas. Las especies alpinas son de fisiología C_3, excepto las tres especies de *Muhlenbergia* que son C_4. Este metabolismo les confiere rasgos anatómicos adicionales que les aseguran su desarrollo en estas zonas.

Epidermis abaxial.—Los caracteres anatómicos diferenciales de las especies alpinas se muestran en el Cuadro 2. Todas las especies alpinas desarrollan ganchos en las regiones costal e intercostal y son de tamaño mediano y base ancha (Figs. 1 y 2). Púas más grandes (Figs. 2, 3 y 4) y de base más ancha que los estomas y se desarrollan sobre el margen. Esta presencia de aguijones (ganchos o púas) refleja la continua condición de sequía a la que las especies están expuestas (Ellis 1979; González-Ledesma et al. 1995; Gómez-Sánchez et al. 2001; Mejía-Saulés y Gómez-Sánchez 2001) y, a mayor estrés hídrico, mayor es la cantidad y el tamaño de los aguijones y el grosor de sus paredes. El estrés hídrico es habitual en las zonas alpinas, pues la disponibilidad de agua se reduce por la congelación y la alta evaporación producida por la intensa radiación solar. Así entonces, la presencia de aguijones, en las especies alpinas, proporciona un mecanismo de protección contra el daño provocado por la insolación proyectando sombra sobre la lámina y reduciendo el calentamiento y la excesiva pérdida de agua. A mayor tamaño y frecuencia de los aguijones, mayor es la sombra que proyectan y se reduce la exposición a la sequía a la que estas especies están expuestas. En *Poa orizabensis* Hitchc. (Fig. 4), *Triniochloa stipoides* (Kunth) Hitchc. (Fig. 13), *Calamagrostis orizabae* (Rupr. ex E. Fourn.) Beal (Fig. 10), *Calamagrostis tolucensis* (Kunth) Trin. ex Steud. (Figs. 2 y 21), *Muhlenbergia nigra* Hitchc. (Fig. 6) y *Muhlenbergia quadridentata* (Kunth) Trin. (Fig. 8) los aguijones son más abundantes y de mayor tamaño que en el resto de las especies alpinas. Esto explica que dichas especies predominen en los zacatonales alpinos (Rzedowski 1978) y se desarrollan en los hábitats de mayor altitud. *Triniochloa stipoides* (Fig. 13) es la única especie con macropelos en su epidermis. Estos resultados sugieren que en el resto de las especies alpinas los micropelos y los macropelos no son necesarios ó bien son remplazados por aguijones.

Las especies alpinas muestran en la epidermis abaxial, una cutícula más gruesa que aquella que se observa en el grupo subalpino, sin embargo, en ambos grupos esa cutícula contribuye a regular la pérdida de agua por evapotranspiración.

Los estomas, en algunas especies, no son visibles (Figs. 2, 5, 8–12) probablemente porque están traslapados y ocultos por los aguijones (Gómez-Sánchez y Koch 1998), porque están embebidos en el mesófilo (Salisbury y Rose 1994) y fueron eliminados durante la preparación de la muestra, o bien, porque los estomas están confinados a los surcos adaxiales de la lámina (Gómez-Sánchez et al. 2001). En cualquiera de estos microambientes la temperatura es menor y los estomas están protegidos, por lo que también se reduce la pérdida de agua por transpiración.

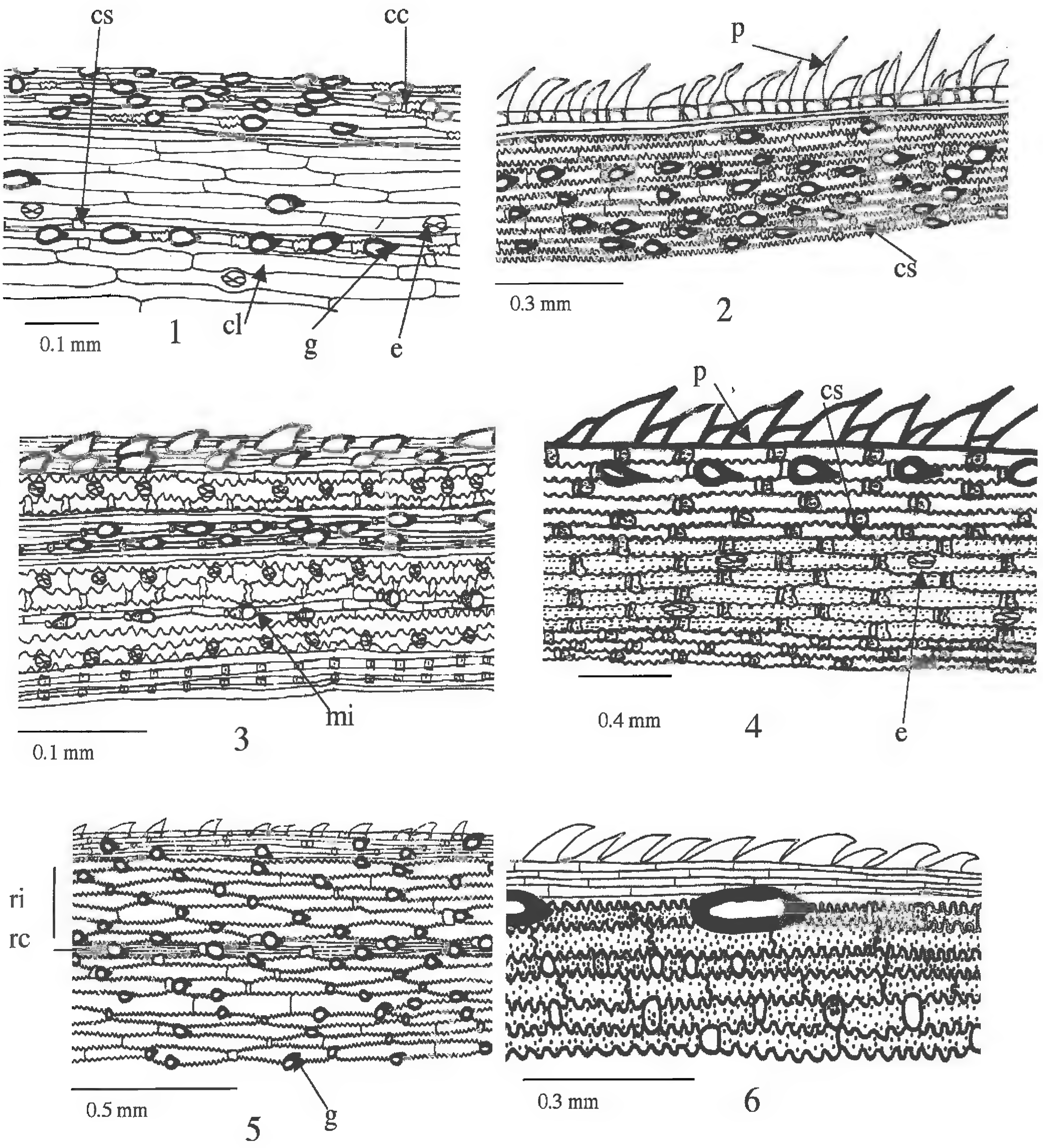
Los cuerpos de sílice son numerosos y más abundantes en las especies alpinas que en las subalpinas y toman formas de hígado (Fig. 5), de pesa (Fig. 8), son redondos (Fig. 6), cuadrados (Fig.1), altos y estrechos

Cuadro 2. Caracteres diferenciales sobre la epidermis abaxial de las especies alpinas. **RC** = región costal. **RI** = región intercostal, **CS** = cuerpos de sílice.

Carácter/especie	***Bromus anomalus***	***Bromus exaltatus***	***Calamagrostis orizabae***	***Calamagrostis tolucensis***	***Deschampsia liebmanniana***	***Festuca hephaestophila***	***Festuca rosei***
Aguijones costales	presentes	presentes	presentes	presentes	presentes	presentes	presentes
Aguijones intercostales	ausentes	presentes	presentes	presentes	presentes	presentes	ausentes
Diferenciación de RC y RI	si	si	no	no	si	si	si
Forma de estomas	elípticos	elípticos	no vistos	no vistos	elípticos	no vistos	no vistos
Disposición de estomas	2 hileras	1 hilera	no vistos	no vistos	1 hilera	no vistos	no vistos
Forma de CS	cuadrados y alargados	cuadrados	cuadrados y alargados	redondos y alargados	hígado y redondos	hígado	hígado
Macropelos	ausentes	ausentes	ausentes	ausentes	ausentes	ausentes	ausentes
Micropelos	ausentes	ausentes	ausentes	ausentes	ausentes	ausentes	ausentes
Paredes anticlinales de células largas	lisas a levemente sinuosas	lisas a levemente sinuosas	Lisas a levemente sinuosas	lisas a profundamente sinuosas	lisas a profundamente sinuosas	Leve a profundamente sinuosas	levemente sinuosas

Cuadro 2 (continuación)

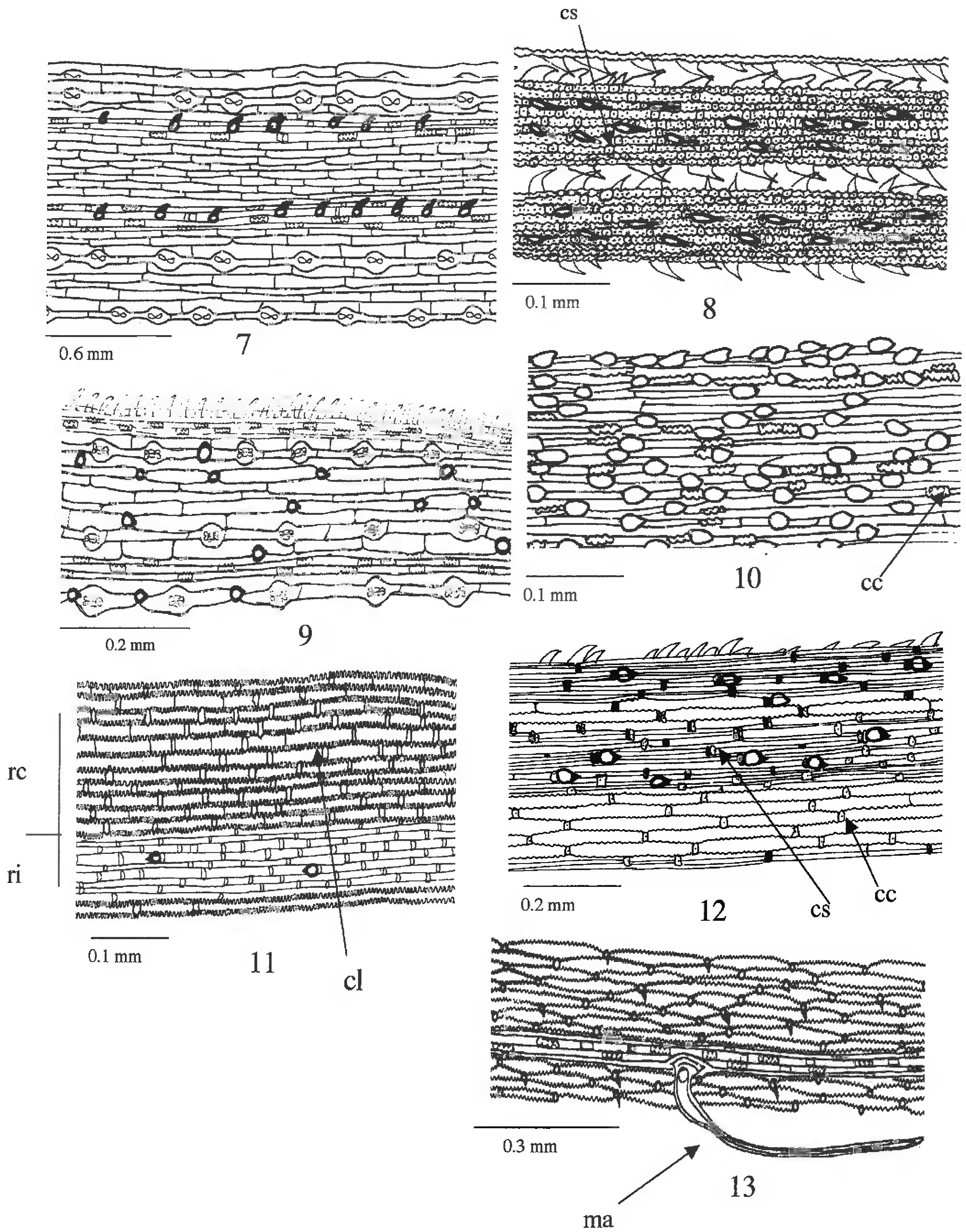
Carácter/especie	***Muhlenbergia quadridentata***	***Muhlenbergia nigra***	***Muhlenbergia orophila***	***Poa orizabensis***	***Triniochloa stipoides***	***Peyritschia koelerioides***
Aguijones costales	presentes	presentes	presentes	presentes	ausentes	ausentes
Aguijones intercostales	no vistos	presentes	ausentes	ausentes	presentes	presentes
Diferenciación de RC y RI	si	si	si	si	si	si
Forma de estomas	no vistos	no vistos	elípticos	elípticos	no vistos	elípticos
Disposición de estomas	no vistos	no vistos	2 hileras	2 hileras	no vistos	2 hileras
Forma de CS	pesa	redondos	cuadrados	hígado y alargados	cuadrados	alargados
Macropelos	ausentes	ausentes	ausentes	ausentes	presentes	ausentes
Micropelos	ausentes	presentes	ausentes	ausentes	ausentes	ausentes
Paredes anticlinales de células largas	Profundamente sinuosas	lisas a profundamente sinuosas	profundamente sinuosas	leve a profundamente sinuosas	lisas a levemente sinuosas	lisas



Figs. 1–6. Epidermis abaxial de la lámina foliar de especies alpinas. 1. ***Bromus exaltatus*** **(*Díaz y Pérez 5963*, IEB). 2.** ***Calamagrostis tolucensis*** **(*Narváez et al. 707*, IEB). 3.** ***Muhlenbergia orophila*** **(*Rzedowski 36012*, ENCB). 4.** ***Poa orizabensis*** **(*Rzedowski 38363*, ENCB). 5.** ***Deschampsia liebmanniana*** **(*Koch 76260*, ENCB). 6.** ***Muhlenbergia nigra*** **(*Koch 280*, ENCB). cc = célula corta, cl = célula larga, cs = cuerpo de sílice, e = estoma, g = gancho, mi = micropelo, p = púa, rc = región costal, ri = región intercostal.**

(Figs. 2 y 4), o alargados (Fig. 10). Este incremento en el número de células de sílice sugiere que la lámina de las especies alpinas está expuesta a una transpiración más alta, pues la presencia y acumulación de sílice es un mecanismo que contribuye con soporte y regula la temperatura de la lámina foliar (Kaufman et al. 1985).

Las paredes anticlinales de las células largas y cortas son lisas (Figs. 1, 7, 9 y 10), moderada (Figs. 8 y 12) o profundamente sinuosas (Figs. 6, 11 y 13). Las paredes anticlinales sinuosas de las células largas y los cuerpos de sílice numerosos brindan rigidez a la lámina (Ellis 1979) y la protegen también contra daños mecánicos provocados por el viento o los animales. *Muhlenbergia orophila* Swallen (Fig. 3), *M. nigra* (Fig. 6), *M. quadridentata* (Fig. 8) y *Festuca hephaestophila* Nees ex Steud. (Fig. 11) muestran células largas con paredes



Figs. 7–13. Epidermis abaxial de la lámina foliar de especies alpinas. **7.** *Bromus anomalus* (*Rzedowski 29299*, ENCB). **8.** *Muhlenbergia quadridentata* (*Cortés 1914*, ENCB). **9.** *Peyritschia koelerioides* (*Rzedowski 41933*, ENCB). **10.** *Calamagrostis orizabae* (*Ventura 1824*, IEB). **11.** *Festuca hephaestophila* (*González y García 90*, IEB). **12.** *F. rosei* (*Pérez Cálix 26*, IEB). **13.** *Triniochloa stipoides* (*Rzedowski 42438*, IEB). cc = célula corta, cl = célula larga, cs = cuerpo de sílice, ma = macropelo, rc = región costal, ri = región intercostal

anticlinales moderada o profundamente sinuosas que brindan rigidez a la lámina lo que sugiere que son especies que resisten fácilmente daños mecánicos provocados por el viento (Ellis 1979).

Estructura interna.— Los caracteres anatómicos diferenciales de la estructura interna que distinguen a las especies alpinas se muestran en el Cuadro 3. El esclerénquima es copioso y forma hebras (Fig. 22) o trabas (Figs. 14, 16, 23 y 25) orientadas adaxial o abaxialmente como una extensión de la vaina de los haces vasculares. Algunas veces, el esclerénquima se desarrolla en bandas (Fig. 18 y 26) que recorren la anchura de la lámina. Su presencia sugiere una baja disponibilidad de agua, que es un elemento importante de sostén, y que evita la apertura total de la lámina impidiendo que ésta tenga una prolongada exposición a la luz solar (Ellis 1976). Las trabas hacen las veces de varillas proporcionando sostén a la lámina y amortiguan los daños mecánicos provocados por los fuertes vientos, pues las fibras ofrecen a la lámina resistencia mecánica y evitan su colapso. Por el contrario, un desarrollo escaso de fibras explica la presencia de culmos laxos y hojas delicadas y frágiles, en gramíneas que habitan ambientes húmedos o menos adversos (Gómez-Sánchez y Koch 1998; Nava-Rojo et al. 2002).

Una quilla conspicua provista de grandes y fuertes trabas o hebras de esclerénquima es evidente en.*Bromus exaltatus* Bernh. (Fig. 14), *Triniochloa stipoides* (Kunth) Hitchc. (Fig. 17), *Poa orizabensis* (Fig. 19), *Deschampsia liebmanniana* (E. Fourn.) Hitchc. (Fig. 22) y *Festuca hephaestophila* Nees ex Steud. (Fig. 24). Esta quilla proporciona sostén y está asociada al control de la pérdida de agua por lo que sugiere que estas especies están expuestas a una excesiva insolación. La lámina foliar de estas especies, a través de la quilla, manifiesta una apertura parcial mostrando una involución en forma de "V." En el resto de las especies alpinas la lámina tiene una involución en forma de "U" o es convoluta, lo cual evita también que la lámina se exponga completamente a la insolación (Ellis 1976; Gómez-Sánchez y Koch 1998; Mejía-Saulés y Gómez-Sánchez 2001) y así regula la pérdida de agua.

Las células buliformes se restringen a los surcos adaxiales, son conspicuas, en forma de abanico (Figs. 14, 16, 23) o son redondas (Figs. 18, 22 y 24). Las trece especies alpinas, estudiadas aquí, muestran células buliformes. Estas células responden a cambios de turgencia provocando la involución de la lámina, mecanismo que regula el paso de luz hacia el mesófilo y la evapotranspiración (Ellis 1979). Estas células no sólo intervienen en la apertura y cierre de la lámina, sino también en la absorción y retención de agua (Tschirch 1882, citado por Ellis 1976). Así entonces, cuando las células buliformes disminuyen su turgencia provocan en la lámina un enrollamiento gradual evitando así que la lámina tenga una excesiva exposición a la luz solar (Ellis 1976, Gómez-Sánchez y Koch 1998). De esta manera, las especies alpinas son beneficiadas porque las células buliformes permiten la involución de la lámina y absorben y retienen agua favoreciendo su supervivencia en los zacatonales alpinos, mismos que están expuestos a una intensa y prolongada insolación y a sequías extremas.

Células incoloras conspicuas dispuestas en columnas que atraviesan el mesófilo se observan en *Muhlenbergia nigra*, *M. orophila* y *M. quadridentata* (Figs. 16, 25 y 26). Estas células incoloras, que frecuentemente están asociadas a las buliformes, funcionan como canales facilitando y regulando el paso de luz hasta las células de clorénquima (Ellis 1976) o las de la vaina Kranz. Esta regulación, además de incidir en un metabolismo eficiente, evita alteraciones al material genético de los cloroplastos, mismas que pudieran ser provocadas si la lámina tuviése una prolongada exposición a los rayos ultravioleta (Ellis 1976; Salisbury y Ross 1994; Gómez-Sánchez y Koch 1998).

Las tres especies de *Muhlenbergia* (Figs. 25 y 26) estudiadas aquí, manifiestan una anatomía Kranz y metabolismo C_4. Estas especies muestran el mesófilo reducido, regularmente dispuesto alrededor de los haces vasculares, estos últimos, están protegidos por una vaina a manera de corona (vaina del haz) de células grandes donde está contenida la mayor parte de los cloroplastos y la presencia de células buliformes e incoloras es importante (Ellis 1976). Estos rasgos permiten que las plantas toleren con éxito las altas temperaturas por una insolación excesiva (Salisbury y Ross 1994). Esta estrategia es común en ambientes como el de los pastizales alpinos o las zonas secas o desérticas, donde la radiación solar es alta y prolongada.

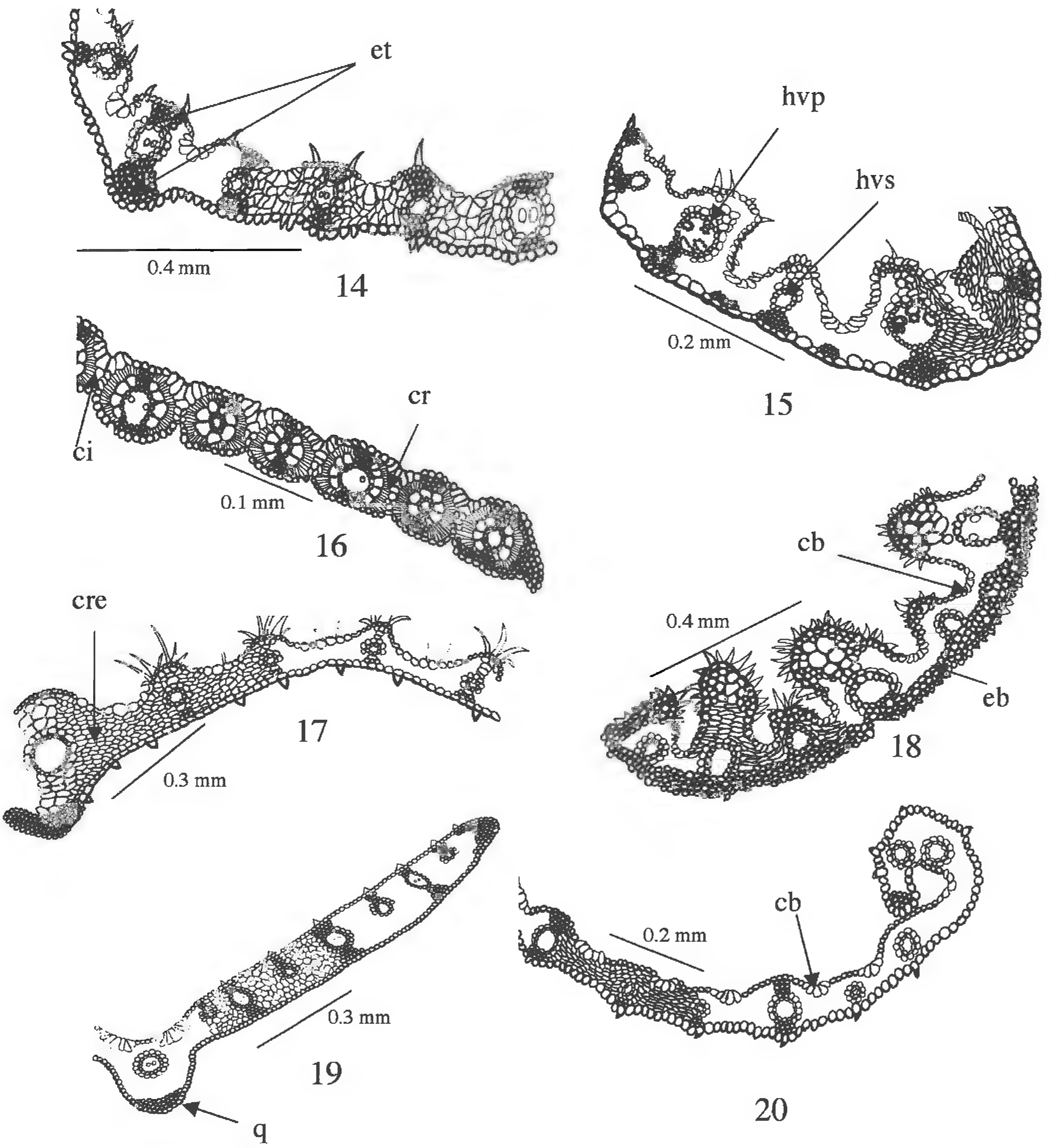
Todas las especies alpinas, excepto *Bromus anomalus* Rupr. ex E. Fourn. y *B. exaltatus* Bernh., tienen

CUADRO 3. Caracteres diferenciales en la estructura interna de las especies alpinas. **ab** = abaxial, **ad** = adaxial, **E** = esclerénquima, **HV** = haces vasculares, **HVP** = haces vasculares primarios, **HVS** = haces vasculares secundarios, **VH** = vaina del haz.

Carácter/especie	***Bromus anomalus***	***Bromus exaltatus***	***Calamagrostis orizabae***	***Calamagrostis tolucensis***	***Deschampsia liebmanniana***	***Festuca hephaestophila***	***Festuca rosei***
Posición de HV en la lámina	central	central	ab	ab	central	central	central
Forma de VH en HVP	redonda	ovada	redonda	redonda	redonda	ovada	redonda
Forma de VH en HVS	redonda	ovada	redonda	redonda	redonda	redonda	redonda
Distribución de E ab en HVP	traba	traba	traba	traba	hebra	hebra	traba
Distribución de E ad en HVP	traba	traba	ausente	hebra	hebra	ausente	hebra
Distribución de E ab en HVS	traba	traba	traba	traba	hebra	hebra	traba
Distribución de E ad en HVS	ausente	traba	hebra	hebra	hebra	ausente	hebra
Distribución de E ab intercostal	ausente	ausente	banda	banda	hebra	ausente	hebra
Banda de E ab.	ausente	ausente	presente	presente	ausente	ausente	ausente
Extensión de la VH	ausente	ausente	ad	presente	ausente	ausente	ad
Interrupción de VH en HVP	ab y ad	ab y ad	ab	ab	ab	ausente	ab
Clorénquima continuo entre HV	presente	presente	presente	presente	presente	presente	presente
Arreglo del clorénquima	irregular	irregular	irregular	irregular	irregular	irregular	irregular
Profundidad de surcos ad.	ausente	ligera	ligera	fuerte	ligera	fuerte	fuerte
Forma de costillas ad.	ausentes	redonda	ovadas	triangulares	triangulares	triangulares	triangulares y ovadas
células incoloras	ausentes	ausentes	ausentes	ausentes	ausentes	ausentes	ausentes
células buliformes	abanico	abanico	redondas	redondas	abanico	redondas	no vistas
Quilla	ausente	ausente	ausente	presente	presente	ausente	Ausente

Cuadro 3 (Continuación)

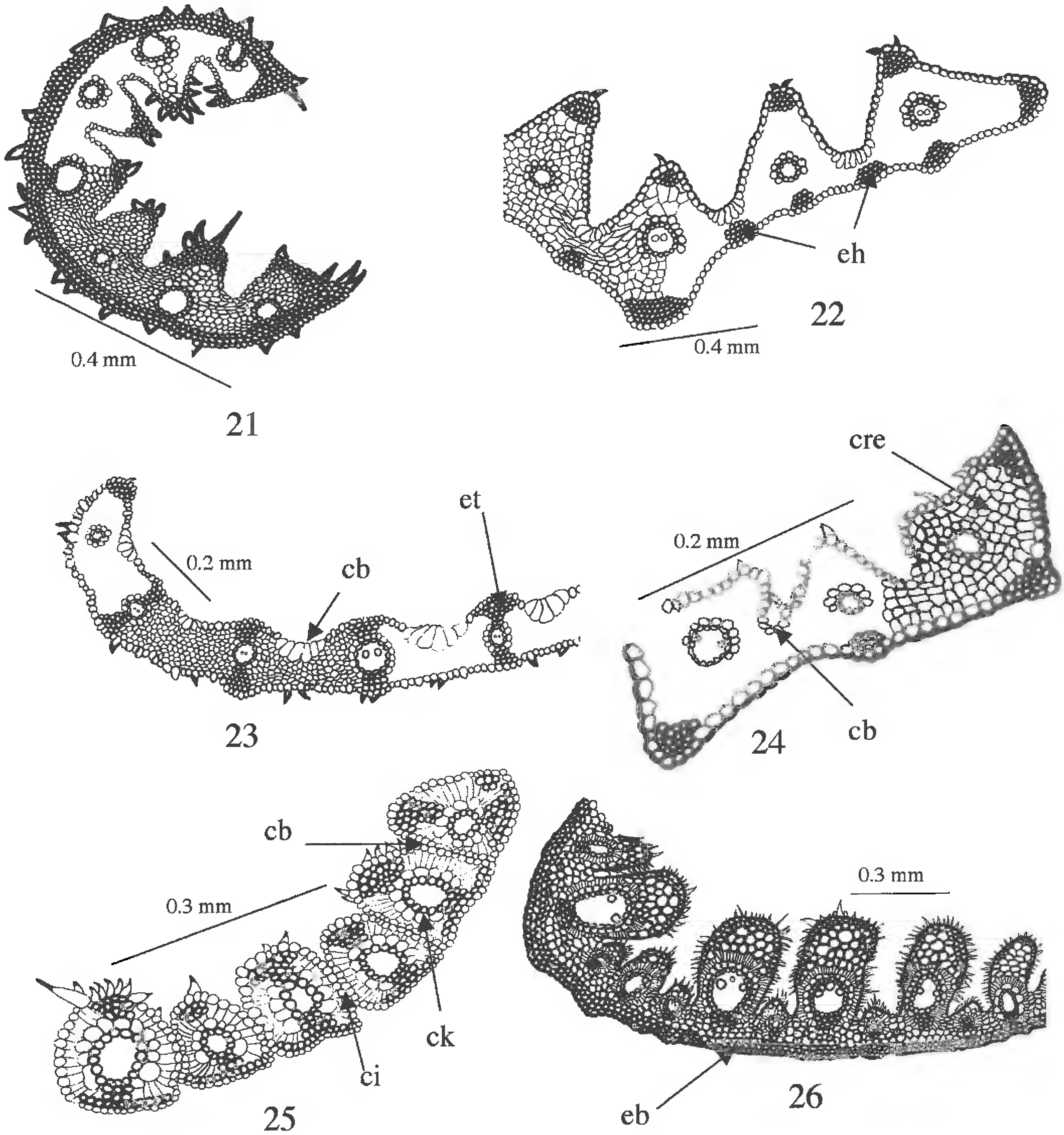
Carácter/especie	*Muhlenbergia quadridentata*	*Muhlenbergia nigra*	*Muhlenbergia orophila*	*Poa orizabensis*	*Triniochloa stipoides*	*Peyritschia koelerioides*
Posición de HV en la lámina	central	central	central	central	central	central
Forma de VH en HVP	ovada	ovada	redonda	redonda	redonda	redonda
Forma de VH en HVS	redonda	ovada	redonda	ovada	redonda	ovada
Distribución de E ab en HVP	traba	hebra	traba	hebra	traba	traba
Distribución de E ad en HVP	traba	hebra	traba	ausente	hebra	traba
Distribución de E ab en HVS	traba	hebra	traba	traba	traba	hebra
Distribución de E ad en HVS	traba	hebra	traba	traba	hebra	traba
Distribución de E ab intercostal	ausente	banda	ausente	ausente	ausente	ausente
Banda de E ab.	ausente	presente	ausente	ausente	ausente	ausente
Extensión de la VH	ausente	ausente	ausente	ab y ad	ab y ad	ausente
Interrupción de VH en HVP	ab y ad	ab	ab y ad	ausente	ausente	ab y ad
Clorénquima continuo entre HV	ausente	presente	ausente	presente	presente	ausente
Arreglo del clorénquima	regular	regular	regular	irregular	irregular	irregular
Profundidad del surco ad.	ligera	fuerte	ausente	ausente	ligera	ligera
Forma de costillas	ovadas	ovada	redondas	ausentes	ovadas	redondas
células incoloras	en columna	en columna	en columna	ausentes	ausentes	ausentes
células buliformes	no vistas	no vistas	abanico	redondas	abanico	abanico
Quilla	ausente	ausente	presente	presente	ausente	presente



Figs. 14–20. Estructura interna de la lámina foliar de especies alpinas. 14. ***Bromus exaltatus*** **(*Díaz Pérez 5963*, IEB). 15.** ***Festuca rosei*** **(*González et al. 26*, IEB). 16.** ***Muhlenbergia orophila*** **(*Herrera 325*, IEB). 17.** ***Triniochloa stipoides*** **(*Rzedowski 42438*, IEB). 18.** ***Calamagrostis orizabae*** **(*Ventura 1824*, IEB). 19.** ***Poa orizabensis*** **(*Koch 75519*, ENCB). 20.** ***Bromus anomalus*** **(*Rzedowski 29299*, ENCB). cb = células buliformes, ci = células incoloras, cr = clorénquima regular (radial), cre = clorénquima irregular (no radial), eb = esclerénquima en banda, et = esclerénquima en traba; hvp = haz vascular primario; hvs = haz vascular secundario, q = quilla.**

hojas más estrechas y delgadas que las subalpinas. Esto sugiere que hay una relación estrecha entre la anchura y el grosor de la lámina y la exposición continua a ambientes secos, aspecto que coincide con Redman (1985, citado por Gómez-Sánchez y Koch 1998) quién determinó que la anchura y el grosor de la hoja están asociados a la resistencia a sequía.

Bromus anomalus y *B. exaltatus* (Figs. 14 y 20), como las demás especies alpinas, desarrollan un esclerénquima copioso que forma trabas abajo y arriba de los haces vasculares, tienen láminas estrechas, células buliformes dispuestas en forma de abanico y poseen aguijones de paredes gruesas y lignificadas



Figs. 21–26. Estructura interna de la lámina foliar de especies alpinas. 21. ***Calamagrostis tolucensis*** **(*Sánchez 85*, IEB). 22.** ***Deschampsia liebmanniana*** **(*Koch 96269*, ENCB). 23.** ***Peyritschia koelerioides*** **(*Rzedowski 41933*, IEB). 24.** ***Festuca hephaestophila*** **(*González y García 151*, IEB). 25.** ***Muhlenbergia quadridentata*** **(*Miranda et al. 894*, IEB). 26.** ***Muhlenbergia nigra*** **(*López-Campos 755*, IEB). cb = células buliformes, ci = células incoloras, cre = clorénquima irregular (no radial), ck = corona Kranz, eh = esclerénquima en hebra, eb = esclerénquima en banda, et = esclerénquima en traba.**

en su estructura interna. No obstante, su epidermis abaxial (Figs. 1 y 7) es semejante a la que se observa en las especies subalpinas. Estos rasgos anatómicofoliares sugieren que, aunque estas especies predominan en lugares altos, cuentan con adaptaciones que les permite sobrevivir a las adversidades del tiempo de las regiones intermedias de los bosques y los pastizales.

Anatomía foliar de gramíneas subalpinas.—Estas especies habitan principalmente en claros ubicados en los bosques de *Pinus*, *Pinus-Quercus* y *Quercus*, desde 1500 hasta 3000 m de altitud, aunque también es posible localizarlas en sitios más altos. Estas plantas son hierbas perennes que forman macollas de aproximadamente 10–40 cm de altura, no obstante, algunos individuos llegan a medir hasta 90 cm ó más. La lámina

foliar de estas especies no desarrollan los mismos mecanismos de protección que las especies alpinas. Sobre la epidermis, los ganchos tienen su base mediana ó más ancha que los estomas y las púas son cortas. En el margen, los ganchos son cortos y de base angosta ó están ausentes en *Agrostis bourgeaei* E. Fourn. y *Phleum alpinum* L. En su estructura interna se identifica el esclerénquima escaso y dispuesto en hebras, a veces se observan pequeñas trabas de 2 a 4 células de ancho abajo de los haces vasculares primarios, el clorénquima es abundante con arreglo irregular y las células buliformes están dispuestas en abanicos pero son pequeñas, a veces son redondas. Todas las especies subalpinas, aquí estudiadas, carecen de células incoloras y de la corona Kranz manifestando una anatomía no-Kranz y metabolismo C_3.

Epidermis abaxial.—Los rasgos anatómicos observados en la epidermis abaxial de las especies subalpinas se describen en el Cuadro 4. El grupo de especies subalpinas, tratadas aquí, contrasta fuertemente con el grupo alpino en la mayoría de sus rasgos anatómicos. En la epidermis de estas especies subalpinas los ganchos son escasos y de tamaño menor (Fig. 27). *Agrostis tolucensis* Kunth y *Festuca tolucensis* Kunth (Figs. 28 y 29) poseen pequeños aguijones de tamaño medio en la región costal. *Poa annua* L. (Fig. 31) exhibe escasos aguijones en el margen de la lámina y, en otras especies los aguijones están ausentes Asimismo, las especies subalpinas carecen de micropelos bicelulares y macropelos. Estos rasgos sugieren que las especies subalpinas no están expuestas a fuertes vientos o heladas frecuentes, como ocurre con las alpinas, por lo que no requieren de una fuerte protección.

El tamaño pequeño de los ganchos y la ausencia de micropelos y macropelos hace suponer que estas especies no requieren evitar la pérdida de agua pues los árboles de los bosques les proveen de sombra, temperatura y humedad estables (Rzedowski 1978) por lo que la evapotranspiración, a través de los estomas, es baja (Salisbury y Ross 1994). La ausencia de aguijones (en la mayoría de las especies), micropelos y macropelos sugiere que estas especies no están expuestas a sequía (Gómez-Sánchez y Koch 1998; Nava-Rojo et al. 2002), o al menos no a condiciones tan adversas como sucede con las especies alpinas. Esta condición contrasta con la presencia de aguijones, micro y macropelos en especies alpinas y también en aquellas de zonas desérticas.

Los estomas están dispuestos en una o varias hileras (Figs. 30 y 31). En ocasiones, los estomas no están visibles, probablemente porque están cubiertos por los escasos aguijones, están inmersos en el mesófilo y éste se eliminó durante el proceso de aislamiento de la epidermis, o bien están confinados a los surcos de la lámina.

En la mayoría de las especies subalpinas, los cuerpos de sílice son escasos y/o pequeños y se observan en forma de hígado (Fig. 33), alargados (Figs. 27, 28 y 32) y redondos o cuadrados (Fig. 34). Este carácter está asociado a las paredes anticlinales de las células largas lisas (Figs. 27, 31 y 32) y ambos rasgos, permiten que las láminas sean laxas y menos rígidas que aquellas de las especies alpinas, lo que coincide con la opinión de Ellis (1979).

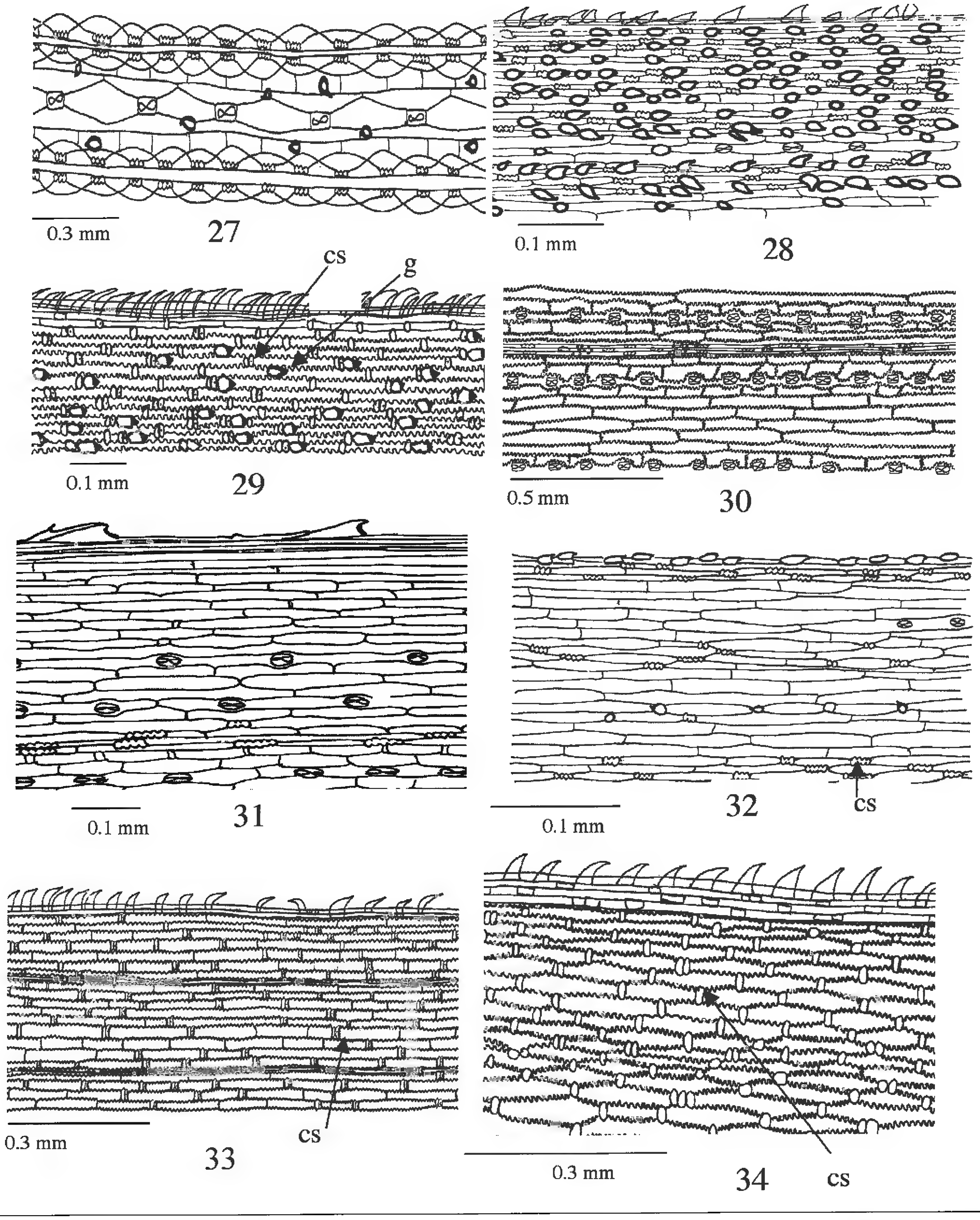
Estructura interna.—Los caracteres anatómicofoliares internos de las especies subalpinas se describen en el Cuadro 5. El esclerénquima es escaso y se desarrolla en hebras, pequeñas trabas de apenas 2–3 células de alto (Figs. 36 y 37) o en banda (Fig. 37). Este desarrollo y disposición del esclerénquima contrasta con el esclerénquima copioso de las especies alpinas. Esto sugiere que las especies subalpinas no necesitan extrema protección contra daños mecánicos.

Las especies subalpinas exhiben clorénquima abundante dispuesto de manera irregular y sus células generalmente son grandes (Figs. 38–40). Las células del mesófilo grandes sugieren que estas especies tienen una buena absorción, retención y disponibilidad de agua.

De acuerdo con el criterio de Ellis (1976), la ausencia de costillas y surcos en la lamina de especies como *Dissanthelium californicum* (Nutt.) Benth. (Fig. 41) o *Poa annua* L. (Fig. 42), o costillas y surcos levemente pronunciadas como en *Festuca tolucensis* Kunth (Fig. 37), se asocian con la apertura completa de la lámina lo que sugiere que estas especies no están expuestas a la radiación solar por periodos prolongados o la intensidad de la luz solar no es extrema. *Festuca livida* (Kunth) Willd. ex Spreng. (Fig. 35) y las tres especies de *Agrostis* (Figs. 38, 39 y 40) muestran surcos y costillas pronunciadas, no obstante, la cantidad

CUADRO 4. Caracteres diferenciales observados en la epidermis abaxial de las especies subalpinas. **CS** = cuerpos de sílice, **RC** = región costal, **RI** = región Intercostal.

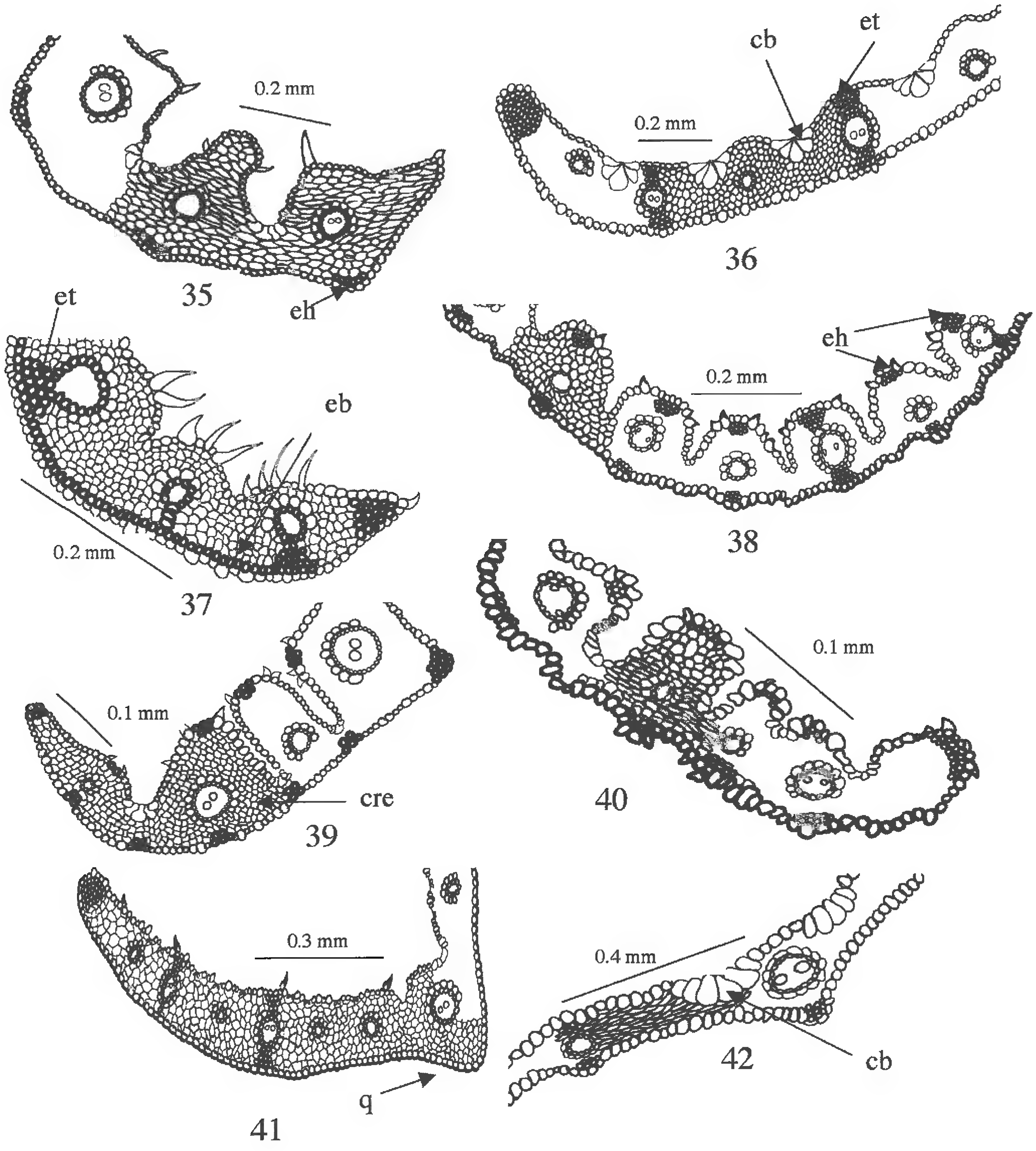
Carácter / especie	*Agrostis bourgei*	*Agrostis tolucensis*	*Agrostis subpatens*	*dissanthelium californicum*	*Festuca tolucensis*	*Festuca livida*	*Phleum alpinum*	*Poa annua*
Aguijones costales	ausentes	presentes	ausentes	presentes	presentes	ausentes	ausentes	ausentes
Aguijones intercostales	presentes	presentes	presentes	presentes	presentes	ausentes	ausentes	ausentes
Diferenciación de RC y RI	si	si	no	si	si	si	si	no
Forma de estomas	cuadrados	elípticos	elípticos	no vistos	elípticos	no vistos	cuadrados	elípticos
Disposición de estomas	1 hilera	1 hilera	1 hilera	no vistos	1 hilera	no vistos	2 hileras	2 hileras
Forma de CS	alargados	alargados	alargados	hígado	hígado	cuadrados y redondos	alargados	alargados
Macropelos	ausentes	ausentes	ausentes	ausentes	ausentes	ausentes	ausentes	ausentes
Micropelos	ausentes	ausentes	ausentes	ausentes	ausentes	ausentes	ausentes	ausentes
Paredes anticlinales de células largas	lisas	lisas	lisas	leve a profundamente sinuosas	leves a profundamente sinuosas	leve a profundamente sinuosas	leve a profundamente sinuosas	lisas



Figs. 27–34. Epidermis abaxial de la lámina foliar de especies subalpinas. 27. *Agrostis bourgeaei* (*Rzedowski 37853*, IEB). 28. *Agrostis tolucensis* (*Rzedowski 23315*, ENCB). 29. *Festuca tolucensis* (*González y Vera 206*, IEB). 30. *Phleum alpinum* (*Rzedowski 25407*, ENCB). 31. *Poa annua* (*Rivas y Campos 41*, IEB). 32. *Agrostis subpatens* (*Rzedowski 36013*, IEB). 33. *Dissanthelium californicum* (*Rzedowski 20174*, ENCB). 34. *Festuca livida* (*González y Hernández 104*, IEB). cs = cuerpo de sílice, g = gancho.

Cuadro 5. Caracteres diferenciales observados en la estructura interna de las especies subalpinas. **Ab** = abaxial, **ad** = adaxial, **E** = esclerénquima, **HV** = haces vasculares, **HVP** = haces primarios, **HVS** = haces vasculares secundarios, **VH** = vaina del haz.

Carácter/especie	***Agrostis bourgeaei***	***Agrostis tolucensis***	***Agrostis subpatens***	***Festuca tolucensis***	***Festuca livida***	***Phleum alpinum***	***Poa annua***	***Dissanthelium californicum***
Posición de HV en la lámina	central	ab	central	central	central	central	central	central
Forma de VH en HVP	ovada	redonda	redonda	redonda	redonda	ovada	redonda	ovada
Forma de VH en HVS	redonda	redonda	redonda	redonda	redonda	redonda	redonda	redonda
Distribución de E ab en HVP	traba	hebra	hebra	traba	hebra	traba	hebra	traba
Distribución de E ad en HVP	traba	hebra	hebra	ausente	ausente	traba	ausente	traba
Distribución de E ab en HVS	hebra	hebra	hebra	traba	hebra	ausente	hebra	ausente
Distribución de E ad en HVS	hebra	hebra	hebra	ausente	ausente	ausente	hebra	ausente
Distribución de E ab intercostal	ausente	ausente	hebra	banda	ausente	ausente	ausente	ausente
Banda de E abaxial	ausente	ausente	ausente	presente	ausente	ausente	ausente	ausente
Extensión de la VH	ausente	ausente	ausente	ausente	ausente	ausente	ausente	ausente
Interrupción de VH en HVP	ab	abaxial	ab	ab	ab	ab y ad	ausente	ab y ad
Clorénquima continuo entre HV	presente	presente	presente	presente	presente	presente	presente	presente
Arreglo del clorénquima	irregular	irregular	irregular	irregular	irregular	irregular	irregular	irregular
Profundidad del surco ad.	fuerte	fuerte	fuerte	ligera	fuerte	ligera	ausente	ausente
Forma de costillas	ovada	triangular y cuadrada	triangular y ovada	ovada	triangular	ovada	ausentes	ausentes
Células incoloras	ausentes	ausentes	ausentes	ausentes	ausentes	ausentes	ausentes	ausentes
Células buliformes	redondas	redondas	abanico	redondas	abanico	abanico	abanico	redondas
Quilla	ausente	ausente	ausente	ausente	ausente	ausente	presente	presente



FIGS. 35–42. Estructura interna de la lámina foliar de especies subalpinas. 35. ***Festuca livida*** **(*Méndez Ibarra 188*, IEB). 36.** ***Phleum alpinum*** **(*Reeder & Reeder 5374*, ENCB). 37.** ***Festuca tolucensis*** **(*González y Vera 206*, IEB). 38.** ***Agrostis bourgeaei*** **(*Rzedowski 25949*, ENCB). 39.** ***Agrostis subpatens*** **(*Rzedowski 36013*, IEB). 40.** ***Agrostis tolucensis*** **(*Rzedowski 41921*, ENCB). 41.** ***Dissanthelium californicum*** **(*Rzedowski 22848*, ENCB). 42.** ***Poa annua*** **(*Morones 052*, IEB). cb = células buliformes, cre = clorénquima irregular (no radial), eb = esclerénquima en banda, eh = esclerénquima en hebra, et = esclerénquima en traba, q = quilla.**

de mesófilo es abundante, las células epidérmicas son grandes y el esclerénquima es escaso, lo que indica que las especies disponen de buena condición hídrica.

Agrostis subpatens Hitchc., *Dissanthelium californicum* y *Poa annua* (Figs. 39, 41 y 42) tienen una quilla, sin embargo, en la primera especie la quilla está provista de una pequeña hebra de esclerénquima, en la segunda el esclerénquima está ausente y, en la tercera, la quilla tiene solamente un pequeño cúmulo de células de esclerénquima. En los tres casos, la quilla solamente es un elemento que da forma a la lámina y proporciona un ligero sostén (Ellis 1976).

Phleum alpinum (Fig. 36) y *Poa annua* (Fig. 42) muestran células buliformes dispuestas en abanico y ocupan la mitad o más de la mitad del grosor de la lámina. No obstante, las células buliformes en la mayoría de las especies subalpinas son de menor tamaño que aquellas de las especies alpinas, lo cual sugiere que la involución de la lámina ocurre en menor grado que en las especies alpinas, puesto que no están expuestas a una pérdida excesiva de agua.

En contraste con el grupo alpino, las especies subalpinas estudiadas carecen de células incoloras y tienen anatomía no-Kranz y metabolismo C_3. Esta condición también es típica en especies que crecen en climas templados y presume que las especies subalpinas reciben luz en cantidad e intensidad adecuadas (Ellis 1976; Hattersley y Watson 1975; Nava-Rojo et al. 2002).

Dissanthelium californicum (Fig. 33), *Festuca livida* (Fig. 34), *F. tolucensis* (Fig. 29) y *Phleum alpinum* (Fig. 30) tienen, en su epidermis, células largas con paredes anticlinales profundamente sinuosas y numerosos cuerpos de sílice como el grupo de especies alpinas. No obstante y como el resto de las especies subalpinas, carecen de aguijones o cuando existen son cortos y de paredes delgadas poco lignificadas, en su estructura interna el esclerénquima es escaso y el mesófilo es conspicuo, mismo que se dispone de manera irregular y sus células son grandes, aumentando así el grosor de la lámina lo que sugiere una presencia de humedad estable (Ellis 1976).

Festuca tolucensis muestra una combinación de caracteres tanto de especies alpinas como de las subalpinas. Esta especie exhibe, en su estructura interna, pequeñas trabas abaxiales de esclerénquima que conectan a los haces vasculares primarios, el clorénquima está ampliamente desarrollado y sus células son grandes dispuestas irregularmente, la involución de la lámina tiene forma de "U" y, las púas y ganchos sobre las caras adaxial y abaxial son grandes y de paredes delgadas (Fig. 37). Sin embargo, el esclerénquima es escaso y ausente de la superficie adaxial de la lámina, los aguijones tienen paredes con escasa lignificación y son cortos como en las especies subalpinas que habitan lugares estables. Esta combinación de caracteres anatómicofoliares sugiere que *F. tolucensis* está adaptada a ambos ambientes lo cual explica su abundancia en los pastizales alpinos y su presencia en claros de bosques de pino-encino (Rzedowski 1978). Situación similar ocurre con *Phleum alpinum*, especie con algunos caracteres de las especies alpinas como el esclerénquima en trabas abaxiales y adaxiales que conectan a los haces vasculares con la epidermis, células buliformes en abanico y paredes anticlinales de las células largas de leve a fuertemente sinuosas (Figs. 30 y 36). No obstante y como las especies subalpinas, carece de cuerpos de sílice o son escasos, los aguijones son cortos y de paredes delgadas, el esclerénquima es escaso, los surcos y costillas adaxiales son apenas notorias y la lámina está expuesta y tiene mayor anchura y grosor.

Existen diferencias anatómicas importantes entre las especies que prosperan en los pastizales alpinos y las que habitan en el interior de los bosques. Las primeras desarrollan mecanismos que las protegen contra diversos daños y se reflejan con claridad en su anatomía foliar. Nuestros resultados sugieren que conforme se avanza en altitud, las condiciones atmosféricas son más agresivas para las especies de gramíneas que habitan las altas montañas, de manera que éstas desarrollan caracteres anatómicos que les permiten permanecer con éxito en esas altitudes y condiciones ecológicas. A partir de un bosque de encino y hacia el pico de una montaña, a mayor altitud mayor es la agresión ambiental y el desarrollo de fibras del esclerénquima se incrementa, el tamaño de las células buliformes es mayor, las células incoloras son conspicuas, la anchura y el grosor de la lámina es menor, el clorénquima y la cantidad de estomas se reducen, y los aguijones aumentan su tamaño y el grosor de sus paredes. Especies, como *Muhlenbergia nigra, M. orophila* y *M. quadridentata* tienen anatomía Kranz y una fisiología alterna, la C_4. Estos rasgos les permiten tolerar las distintas condiciones extremas (Ellis 1977 y Salisbury y Ross 1994) que prosperan en estos ambientes de alta montaña. Dadas las condiciones tan especiales que imperan en los ambientes de alta montaña, es posible que otras especies alpinas y subalpinas tengan distintos patrones anatómicos a los descritos aquí, lo cual podría confirmarse estudiando un número más amplio de especies.

APÉNDICE 1
ESPECÍMENES REVISADOS

Agrostis bourgeaei E. Fourn. **MÉXICO. Ixtapaluca:** estación experimental de investigación y enseñanza de Zoquiapan, 8 km al sur de Río Frío, S. D. *Koch 75328* (ENCB). **Ixtapaluca:** estación experimental de investigación y enseñanza de Zoquiapan, 8 km al sur de río Frío, *Vega 186* (ENCB). **Tlalmanalco:** La Ciénega, región de Peñas Cuatas, *S. Acosta 961* (ENCB). **Ayucan:** 3 km al NW de San Luis Ayucan, *Acosta 35955* (IEB). **Iturbide:** alrededores de la presa Iturbide, *Rzedowski 38021* (IEB). *Agrostis subpatens* Hitchc. **MÉXICO**. alrededores de la Joya de Alcalican, *Rzedowski 36013* (IEB). *Agrostis tolucensis* Kunth. **MÉXICO. Amecameca:** la Joya de Alcalican, *Castellanos s.n.* (IEB). **Tlacotepec:** Cerro Teotepec, *Rzedowski 18147* (ENCB). **DISTRITO FEDERAL. Deleg. Cuajimalpa:** Puerto de las Cruces, *Herrera 288* (IEB). **MICHOACÁN. Huiramba:** parte alta del Cerro del Burro, *Rzedowski 41921* (IEB). **Angangueo:** camino al vivero Sierra de Chincua, *Macaria Mejía s.n.* (IEB). *Bromus anomalus* Rupr.ex. E. Fourn. **HIDALGO. Zempoala:** Sierra de los Pitos, *Benítez 277* (ENCB), 5 km al N de Atizapán, *Rzedowski 20921* (ENCB). *Bromas exaltatus* Bernh. **MÉXICO. Ixtapaluca:** Estación de investigación y enseñanza Zoquiapan, carretera Mèxico-Puebla, 8 km, al S de rìo Frìo, camino 5, *Vega 288* (ENCB). **HIDALGO. El Chico:** cerro de Las Ventanas (sierra de Pachuca), *Vera 777* (ENCB). *Calamagrostis oriabae* (Rupr. ex E. Fourn) Beal. *Ventura 1824* (IEB) (sin registro de lugar de colecta). *Calamagrostis tolucensis* (Kunth) Trin. ex Steud. **México. Ixtapaluca:** cerro Tláloc, *Flores 288* (IEB). **San Mateo:** a 2.4 km de la desviación al Nevado de Toluca, *Manrique et al. 271* (IEB). **Tlalmanalco:** la Ciénega, región de la cabeza del Ixtaccíhuatl, *Rzedowski 37689* (ENCB). **Santa Ana Xilotzingo:** alrededores del Llano de la Horca, *Rzedowski 31668* (ENCB). **PUEBLA:** 2.3 km a Río Frío, barranca entre supercarretera y carretera libre México-Puebla, *Weber 541* (ENCB). **DISTRITO FEDERAL:** ladera E del Cerro Pelado, serranía del Ajusco, *Rzedowski 12626a* (ENCB). *Deschampsia liebmanniana* (E. Fourn.) Hitchc. **MÉXICO. Tlalmanalco:** alrededores del Llano Grande, arriba de san Rafael, *Rzedowski 38266* (ENCB). **La Ciénega:** región de Peñas Cuatas, cerca de la cabeza del Ixtaccíhuatl, *Rzedowski 37189* (IEB). Vertiente SW del Ixtaccíhuatl, 4 km al N de la estación retransmisora, *Rzedowski 20163* (ENCB. **MICHOACÁN. Santa Clara del Cobre:** La Laguna, cerca de San Gregorio, *Santos 1014* (ENCB). **Tancítaro:** above apo on cerro Tancítaro, *Geredu 585* (ENCB). **DISTRITO FEDERAL:** alrededores de la estación La Cima, serranía del Ajusco, *Rzedowski 12597* (ENCB). *Dissanthelium californicum* (Nutt.) Benth. **MÉXICO. Texcoco:** Cerro Tláloc. **Sierra Nevada:** zona alpina, pradera alpina con *C. tolucensis* y *Festuca tolucensis*. *Wendt y Atkinson 3950* (ENCB). *Festuca hephaestophila* Nees ex Steud. **MÉXICO. Ixtapaluca:** estación experimental de investigación y enseñanza de Zoquiapan, 8 km al S de Río Frío, *González et al. 99* (IEB). *Festuca livida* (Kunth) Willd. ex Spreng. *González y Hernández 104* (IEB), *Méndez 188* (IEB). Sin registro de colecta. *Festuca rosei* Piper. **MICHOACÁN. Santa Clara del Cobre:** cerro El Frijol, al N de Santa Juana, *Pérez 690* (IEB). *Festuca tolucensis* Kunth. **MICHOACÁN. Zinapécuaro:** parte alta del cerro San Andrés, *Zamudio 5586* (IEB). **MÉXICO. Amecameca:** la Joya de Alcalican, *Cruz 14* (IEB). *Muhlenbergia nigra* Hitchc. **MÉXICO. Amecameca:** 10 km al E de Amecameca, sobre el camino a Tlamacas, *Rzedowski s.n.* (ENCB). **MICHOACÁN. Quiroga:** cerro del Tzirate, *López 755* (IEB). *Muhlenbergia orophila Swallen.* **DISTRITO FEDERAL. Cuajimalpa:** Puerto de las Cruces, *Herrera 325* (IEB). *Muhlenbergia quadridentata* (Kunth) Trin. **PUEBLA:** Ladera E del Popocatépetl, 10 km al W de Santiago Salicinta, *Herrera y Cortés 917* (IEB). **MÉXICO:** Parque Nacional La Marqueza, 1 km al S de la Marqueza, *Herrera y Cortés 929* (IEB). **MÉXICO:** a 7.2 km de la desviación al Nevado de Toluca, carretera Toluca-Temascaltepec, *Manrique et al. 260* (IEB). **MÉXICO. Amecameca**, La Joya de Alcalican, *Magallón B. 1319* (IEB). **MICHOACÁN. Quiroga:** cerro del Tzirate, *López 1176* (IEB). **MÉXICO. Ixtapaluca:** estación experimental de investigación y enseñanza de Zoquiapan. 8 km al S de Río Frío, *Vega 135* (ENCB). **DISTRITO FEDERAL. Milpa Alta:** cerro Tilcoayo, *Miranda et al. 894* (IEB). *Peyritschia koelerioides* (Peyr.) E. Fourn. **MICHOACÁN. Huiramba:** parte alta del Cerro del Burro, *Rzedowski 41933* (IEB). *Phleum alpinum* L. **VERACRUZ. Perote:** Cofre de Perote, lado N en la base del macizo de roca que se encuentra en la cima del Cofre de Perote, *González et al.136* (ENCB). *Poa annua* L. **MÉXICO. La Joya de Alcalican:** parte SW del Ixtaccíhuatl, *Rzedowski 25676* (IEB). **Amecameca:** 10 km al E de Amecameca, *Jiménez 76* (IEB). **Ixtapaluca:** Est. Exp. de Inv. de Zoquiapan, 8 km al S de Río Frío, *Koch 75519* (ENCB). **HIDALGO. Epazoyucan:** 3 km al SE de Real del Monte, *Medina-Cota 1466* (IEB). **DISTRITO FEDERAL:** claros cercanos al 4º dinamo de c/treras, *Rzedowski 20381* (IEB), **Tlalpan:** Cerro del Ajusco, *Bojorquez s.n.* (IEB). **VERACRUZ. Calcahualco:** 8 km al O de Calcahualco, *Mejía-Sauléz 1151* (IEB). **MICHOACÁN. Pátzcuaro:** Joya de Las Navas, *Escobedo 669* (IEB). **JALISCO. Mazamitla:** a 6 km de Mazamitla por brecha a microondas El Montoso, *Morones G. 052* (IEB). *Poa orizabensis* Hitchc. **MËXICO. Ixtapaluca:** Estación Experimental de Investigación y Enseñanza de Zoquiapan , 8 km al S de Río Frío, *Koch 75519* (ENCB). *Triniochloa stipoides* (Kunth) Hitchc. **PUEBLA. Zacapoaxtla:** 8 km después de Zaragoza rumbo a Zacapoaxtla, *Núñez et al. 369* (COCA). **MICHOACÁN:** cerca de Pontezuela, 25 km al E de Morelia, sobre la carretera a Mil Cumbres, *Rzedowski 42438* (IEB). **MICHOACÁN. Pátzcuaro:** cerro Los Lobos, sobre carretera Pátzcuaro-Morelia, *Díaz 1670* (IEB). **MICHOACÁN. Pátzcuaro:** Joya de Las Navas, *Escobedo 661* (IEB). **GUANAJUATO. Jenécuaro:** terrenos pertenecientes a El Tejocote, *Rzedowski 50574* (IEB). **MICHOACÁN. Nahuatzen:** Cerros Pelón y Cherán de la Mojonera, *Martínez 402* (IEB). **Nahuatzen y Tingambato:** cerro La Bandera, cerca de Comachuen, *Martínez 752* (IEB). **Michoacán:** 19 km al E de Querétaro, sobre la carretera a Maravatio, *Rzedowski 40993* (IEB). **GUANAJUATO. Guanajuato:** 3 km al NE de Santa. Rosa. *Rzedowski 42044* (IEB). **QUERÉTARO. Pinal de Amoles:** al W de la cuesta de Huazmazantla, *carranza 2926* (IEB). **Pinal de amoles:** al S de los Pinos, *Carranza 2912* (IEB). **VERACRUZ:** Las Vigas, Los Hermanos, *Ventura 4306* (ENCB). **OAXACA. Sola de Vega:** carretera Puerto Escondido, 13 km al S de Sola de Vega, *Koch et al 79559* (CHAPA). **GUERRERO:** Heidoro, 68 km de filo de caballo por terracería a El Paraíso, *González-Ledesma et al. 487* (CHAPA). **NUEVO LEÓN. Zaragoza:** 9 km de Zaragoza por camino de terracería a La Encantada, *González-Ledesma y García 683* (CHAPA).

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BOOK NOTICE

Rafaël Govaerts, Paul Wilkin, and Richard M.K. Saunders. 2007. **World Checklist of Dioscoreales: Yams and Their Allies.** (ISBN 978-1-84246-200-3, pbk.). Royal Botanic Gardens, Kew, Richmond, Surrey, TW9 3AB, United Kingdom. (**Orders:** www.kewbooks.com, publishing@kew.org). $50.00, 65 pp., 9" × 6".

Contents:

- Introduction
- How to use the Checklist
  - Structure
  - Names
  - Acceptance of taxa
  - Geographical distribution
  - Life-forms
- Abbreviations
- References
- Acknowledgments
- Burmanniaceae
- Dioscoreaceae
- Nartheciaceae

From the publishers.—"Dioscoreales are a small but systematically and economically significant order of monocotyledons. The most diverse and important member is the yam genus, *Dioscorea* L., a source of dietary starch at macroeconomic to rural community levels. Other species of *Dioscorea* provided the chemical basis of corticosteroid drugs and oral contraceptives. Ally families comprise the unusual, largely achlorophyllous (heteromycotrophic) Burmanniaceae and the relatively unspecialised Nartheciaceae...The book lists all names ever published; lists all accepted species with their geographical distribution; indicates full synonymy, provides a single source guide to the correct names of all yams and their allies; and provides an invaluable reference for applied yam researchers, e.g., pathologists, geneticists, plant breeders, conservationists, foresters, ethnobotanists, ethnoarchaeologists and anthropologists."

A NOVEL DESIGN FOR A LIGHT WEIGHT AND DURABLE FIELD PRESS

Charles T. Bryson

USDA-ARS
Southern Weed Science Laboratory
P.O. Box 350
Stoneville, Mississippi 38776, U.S.A.
charles.bryson@ars.usda.gov

Richard Carter

Herbarium
Biology Department
Valdosta State University
Valdosta, Georgia 31698-0015, U.S.A.
rcarter@valdosta.edu

ABSTRACT

The development of a light weight, washable, durable, and inexpensive field press is described and illustrated. A pattern and protocol for construction of the field press are provided as well as instructions for its use.

RESUMEN

Se describe e ilustra un aparato portátil para prensar especímenes vegetales en el campo, hecho de material ligero, resistente y barato. Se aporta un patrón y el protocolo para construir la prensa junto con una guía para su uso.

As long as Botanists have collected plants, new and innovative methods have been developed to dry and preserve specimens that retain as much of the natural integrity of the living plant as possible (cf. Smith et al. 1886). Results of the progress in pressing, drying, and preserving methods are readily apparent upon viewing a series of herbarium specimens covering several generations of botanical collectors. The standard methodology employing newsprint, blotters, corrugated cardboard, and heat has been used for several decades to dry specimens, and details about composition, construction, and procedures for drying specimens are provided by a number of authors (e.g., Fosberg & Sachet 1965; Simpson 2006; Carter et al. 2007).

Various materials and methods including metal tubes or cans (vascula), cloth sacks, Styrofoam ice chests, and paper and plastic bags have been used to transport specimens from the field to drying presses, Alternatively, heavy and cumbersome drying presses may be taken directly to the field; however, their use is often prohibited by terrain, distances traversed, and adverse weather conditions. Several field press (portfolio) designs have been used over the years, including that of Fosberg and Sachet (1965). Haynes (2006) described a field press made from several pieces of cardboard corrugate cinched with a press strap. In the early 1990s, Dr. Anton A. Reznicek, curator of vascular plants at the University of Michigan, constructed a field press of cardboard and duct tape and secured with a cord, which was light weight and easy to use under most field conditions. During a field trip to central Arkansas in 1993 with Dr. Reznicek, Dr. Paul Rothrock, and Philip Hyatt, Dr. Reznicek was observed using a cardboard and rope press. Immediately after this field trip, the senior author constructed a prototype of the press described herein out of heavy cloth and rope. Over the years this cloth press has been modified to increase the ease of use and to perfect the overall dimensions. The second author has successfully improvised a variation on Dr. Reznicek's field press by cutting down corners of a cardboard carton and using the sides and top flaps, still attached, to hold specimens enfolded in newsprint.

MATERIALS AND METHODS

Instructions and materials for making the Bryson Field Press (Fig. 1)

1. Cut out two pieces of cotton canvas or similar weight cotton cloth, one piece 1 to 1.5 m long and 0.35 m wide and one piece 0.9 to 1.0 m long and 0.5 m wide.
2. Place cloth right side down.
3. To create hem, turn edges over 1.5 cm and fold over again, then pin hems to hold in place (Fig. 1, hem inset).
4. Clip small triangle at end of each piece of cloth, then fold the miter corners with double folds and pin (Fig. 1, corner insets).

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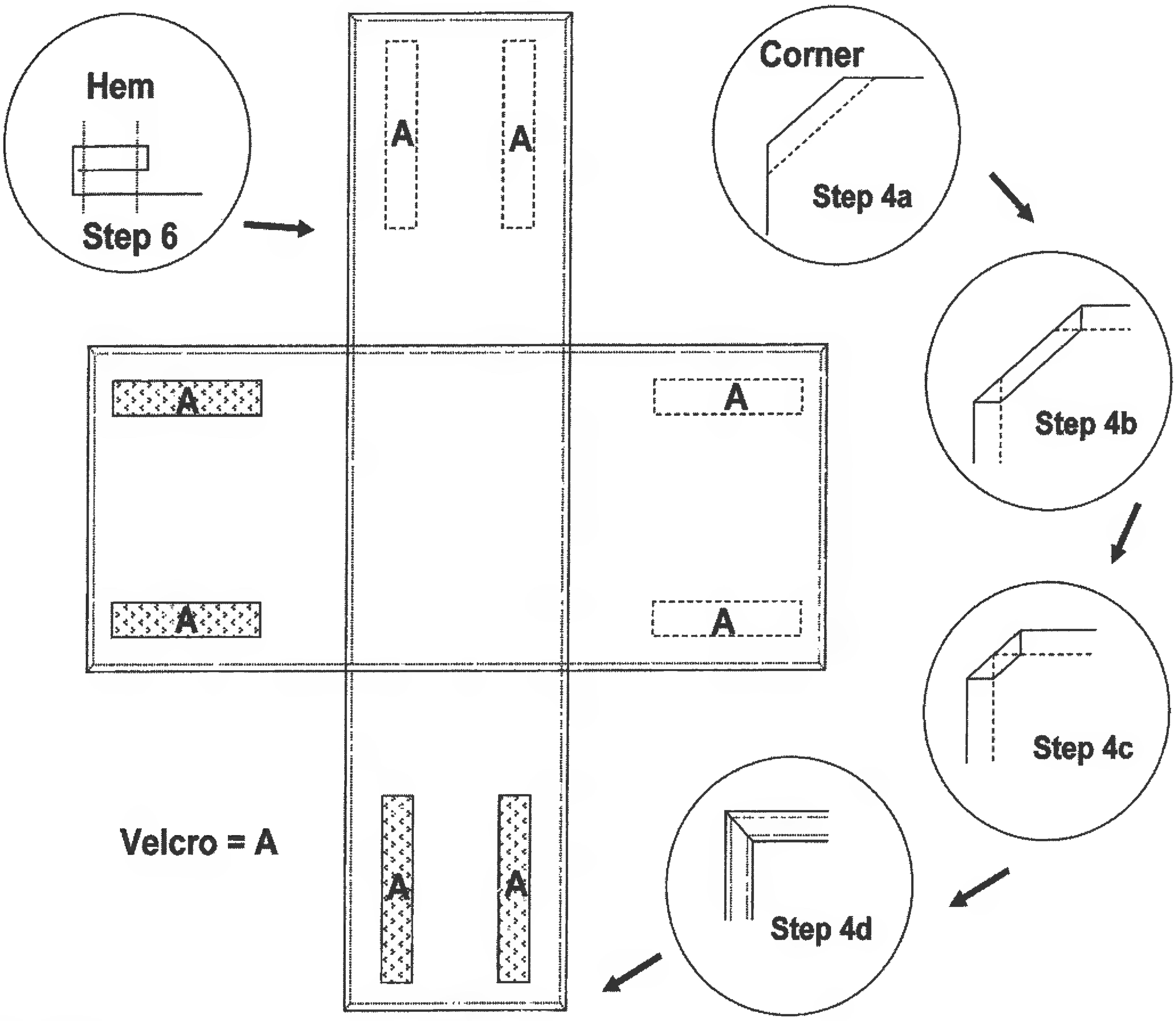

Fig. 1. Diagram of the Bryson Field Press.

5. Iron hem and corners prior to sewing.
6. Stitch around each hem and corner twice on the inside and twice near the outside edge and tie thread ends.
7. Cross pieces with hem side up and cloth right side down forming equal size opposing flaps.
8. Pin the two pieces together.
9. Sew the two pieces together by stitching over previous hem stitches where the pieces overlap and tie thread ends. One side can be left open to create a pocket for a record book, piece of sturdy corrugated cardboard, plywood, or other field supplies.
10. Pin Velcro to the cloth using care to align corresponding pieces on each side. Note that Velcro strips are attached to opposite sides of the cloth on opposing flaps.
11. Stitch around the edge of each piece of Velcro twice and tie thread ends. Strips of Velcro at least 5 cm wide provide better field press closure than narrower strips.
12. Remove all pins and the field press is ready to use.

DISCUSSION

The field press described herein (Fig. 1) is the result of over 15 years of field testing by the authors and except for its size and more permanent materials is based on Dr. Reznicek's initial concept. Durable, light weight, and washable, it is easy to use in a variety of field situations (Fig. 2). The press can be carried under the arm or attached to a back pack, an all terrain vehicle (ATV), or a saddle. It is also convenient for press-

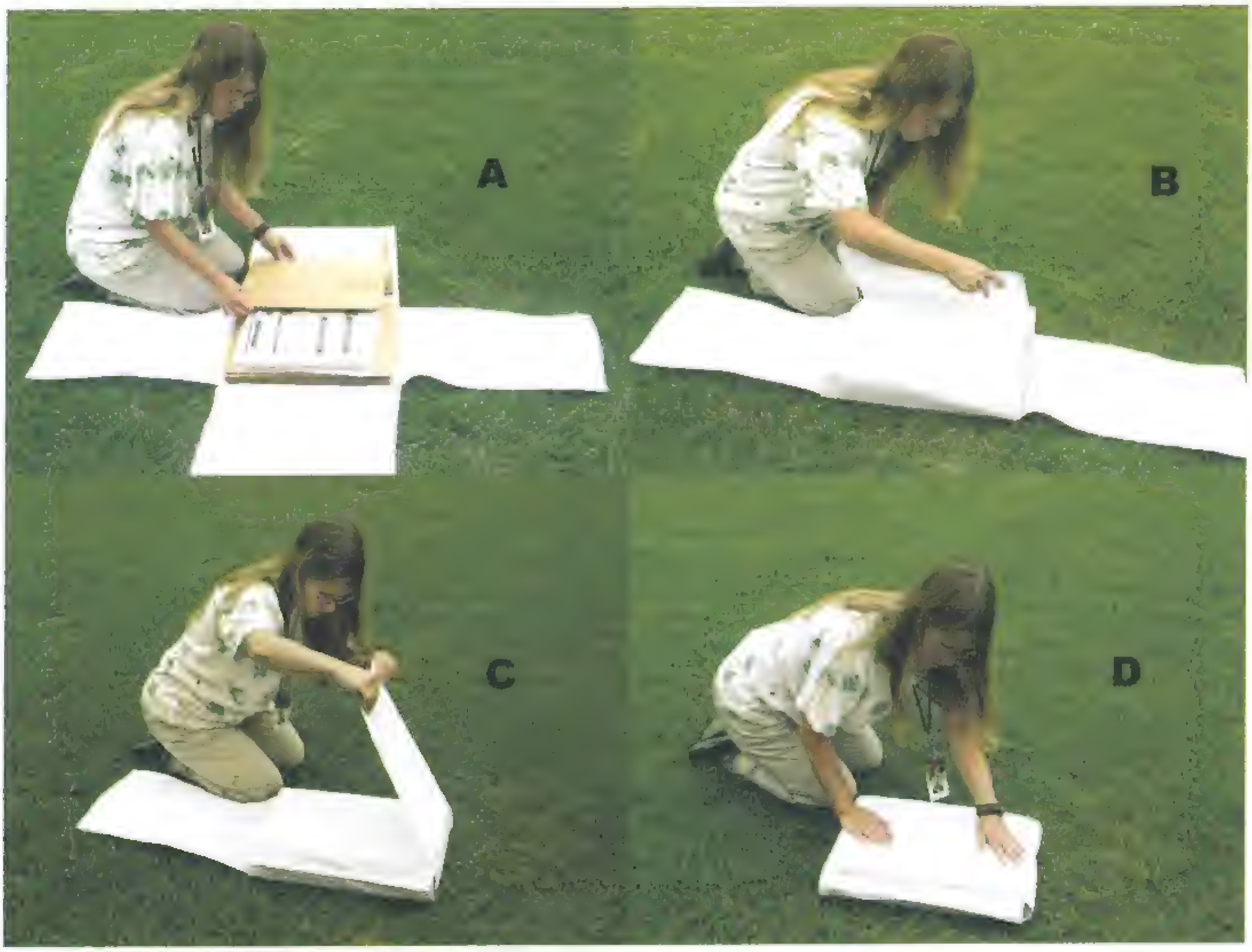

Fig. 2. Photos illustrating the Bryson Field Press (A, loading the field press; B, closing the first set of flaps; C, closing the second set of flaps; and D, closed field press).

ing and transporting plants in a boat or canoe where a conventional press is too heavy or bulky. It is useful for pressing large numbers of specimens rapidly and for pressing plants that wilt rapidly or lose floral parts upon harvesting. The capacity of the press varies depending on the length of the press flaps and thickness of plant specimens and materials used to divide the specimens; however, we have stacked more than 100 specimens in a single field press. The porous cotton fabric allows the press to "breathe" and the drying process to begin. Whereas other materials, such as treated canvas, plastic lined cloth, or heavy plastic were tried in several prototypes, these materials proved to be unacceptable, because they prevented drying and increased condensation, promoted mold and mildew growth, and caused discoloration of specimens. However, heavy weight polyester or other synthetic fabric may be substituted for cotton to make the field press suitable for field work in tropical areas or environments with constant moisture. Although extra cardboard corrugates, plywood, or felt blotters add weight and bulk, they can be used in the field press. Three heavy pieces of corrugated cardboard (one on top, one on bottom, and one between newsprint and the pressed specimens) provide the lightest weight, while allowing for adequate handling of specimens. Additional corrugates can be used to separate specimens from different collection sites or to separate pre-numbered and unnumbered newsprint. We developed a system of pressing the first specimen in pre-numbered newsprint and the duplicates in unnumbered newsprint. When these are placed into a conventional drying press from the top to bottom of each stack from the field press, the numbered newsprint is removed first from the conventional drying press. Thus, the duplicates can be easily tucked into the folded numbered sheet. Unknown to us, Dr. John Thieret and his students used a similar numbering technique (Haynes 2006).

A reasonably skilled seamstress can cut out, pin, and sew a field press in about two hours. The major expenses in constructing one of these presses are the fabric and Velcro. Blemished and seconds fabric can be purchased to save in the overall cost. Also, we have noted that lighter colored fabrics absorb less heat from sunlight than darker colored fabrics. Although wider Velcro strips are substantially more expensive, Velcro strips at least 5 cm wide provide better closure than narrower strips. The estimated cost of fabric, Velcro, and thread is $20.00 to $35.00 per press, but may vary depending on the price and weight of the fabric and amount and width of Velcro. The first author experimented with addition of expandable pockets for temporarily storing woody stems and fruit and straps or handles for carrying the press in the field similar to commercially available presses. Each of these modifications may provide better utility for specific situations, but add cost and bulk to the simple design described herewith.

Specimens are pressed between newsprint and stacked on top of one another with one piece of corrugated cardboard on the top and another piece on the bottom of the stack. The press is closed and secured by pressing the Velcro strips on the first set of flaps against those on the opposing set. Next the second set of opposing flaps is closed and secured. Two sets of opposing flaps allow for greater pressure on the stacked specimens, hold specimens in place within the newsprint, and provide pressure on plant parts that were folded over in fitting the specimen to newsprint sheets. With this field press, unlike vascula, cloth sacks, Styrofoam ice chests, and paper or plastic bags, specimens are in the exact order in which they were collected, facilitating correlation with field notes. When field work is completed, the newsprint folds containing specimens are removed and placed into a standard drying press. While placing the specimens in the drying press, they can easily be repositioned as needed, e.g. refolding leaves or other plant parts to expose flowers, fruits or other structures. Precautions should be taken to keep loaded field presses as cool as possible and out of direct sunlight. For optimal results, plants should be taken from the field press and placed in drying presses as soon as possible, e.g. at the end of each day. However, the time in the field press can be extended depending upon environmental conditions and the kinds of plants being pressed. Plants such as grasses and sedges may remain in the field press longer than plants that are subject to discoloration or contain high water content, and specimens may be kept in the field press under refrigeration overnight with no discernable ill effects. Although not recommended, in unusual circumstances of exigency, we have kept specimens in a field press for almost a week.

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STRUCTURE AND DIVERSITY OF A RIPARIAN FOREST AT KAIETEUR NATIONAL PARK, GUYANA

Carol L. Kelloff

Department of Botany, MRC166
10th and Constitution Ave, NW
P.O. Box 37012
Smithsonian Institution, NMNH
Washington, DC 20013-7012, U.S.A.
email: kelloffc@si.edu

ABSTRACT

Kaieteur National Park, encompassing middle portions of the Potaro River, Guyana, contains a mosaic of habitats from exposed sandstone to riparian forests (100 – 450 m) with soils of the riparian forests of course white sand with very little peat. As part of an ecological study, two one-hectare plots were established in the Wallaba (*Eperua*)–mixed forest of the Potaro Plateau to document the species diversity and tree composition within the park. Approximately 133 species in 33 families comprised 1585 trees with a DBH ≥ 10 cm. *Chamaecrista adiantifolia* var. *pteridophylla* and *Eperua falcata* (Leguminosae-Caesalpinioideae) accounted for 26.1% of all trees inventoried in the plots. Of the three subfamilies of Leguminosae, Caesalpinioideae had over 300 stems/ha at Kaieteur. We used two 1 ha plots at each site to compare the forest at Kaieteur with the lowland forest of Kwakwani (Guyana) and Barro Colorado Island (Panama). Of these three, Kaieteur had the highest number of stems (69.6%) < 20 cm DBH and highest total basal area (66 m^2 / ha). Statistical analysis of the two plots at Kaieteur clearly indicates a high degree of floristic differences between the Kaieteur sites in this Wallaba (*Eperua*)–mixed forest. Although dominated by *E. falcata* and *C. adiantifolia* var. *pteridophylla*, the plots at Kaieteur indicate there are differences in the forest community over a very short distance. This may be attributable to subtle changes in microhabitats and/or species dynamics of the subdominant tree taxa of the Potaro Plateau.

KEY WORDS: Barro Colorado Island, Guiana Shield, Kwakwani, Pakaraima Mountains, plots, Roraima sandstone

RESUMEN

El Parque Nacional de Kaieteur localizado a lo largo del curso medio del río Potaro en Guyana, es un mosaico de hábitats que incluye desde areniscas expuestas hasta bosques ribereños (100–450 m) con suelos de arenas blancas con muy bajos contenidos de materia orgánica. Como parte de un estudio ecológico, se instalaron dos parcelas de 1 ha en el Wallaba (*Eperua*)-bosque mixto del altiplano de Potaro - a los efectos de documentar la diversidad especifica y la composición del dosel arbóreo dentro del Parque. En ambas parcelas se encontraron un total de 1585 individuos con DAP mayor a 10 cm, los que se correspondieron con aproximadamente 133 especies reunidas en 33 familias. *Chamaecrista adiantifolia* var. *pteridophylla* y *Eperua falcata* (Leguminosae-Caesalpinoideae) constituyeron el 26.1% del total de los tallos inventariados. De las tres subfamilias de Leguminosas, Caesalpinoideae fue la mejor representada en las parcelas de Kaieteur, con mas de 300 tallos/ha. Utilizamos parcelas de 1 ha para comparar el bosque de Kaieteur con los bosques de tierras bajas ubicados en Kwakwani (Guyana) y en la Isla de Barro Colorado (Panamá). De los tres bosques comparados, Kaieteur tuvo el mayor numero de tallos (69.6%) con DAP menores a los 20 cm, y la mayor área basal total (66 m^2/ha). El análisis estadístico de las dos parcelas en Kaieteur indican claramente que existen grandes diferencias florísticas entres ellas. Auque ambas parcelas son dominadas por *E. falcata* y *C. adiantifolia* var. *pteridophylla*, estas muestran diferencias en la composición y estructura a lo largo de cortas distancias. Estas diferencias pueden deberse a cambios sutiles de microhábitat y/o a las diferentes interacciones entre las especies de árboles sub-dominantes del altiplano de Potaro.

INTRODUCTION

Kaieteur National Park (Fig. 1), the only national park in Guyana, is located approximately 230 km southwest (5° 10' 42" N; 59° 29' 44" W) of Georgetown, the nation's capital. The park is situated on an upland region of Guyana known as the Potaro Plateau of the Pakaraima Mountains. This plateau is an eastern extension of the largely Venezuelan Roraima sandstone formation that forms the flat table-top mountains known as tepuis. The Potaro River flowing over this plateau has cut a 20 km gorge in the easternmost portion of the Roraima formation. The river eventually plunges 226 meters via a single drop into the gorge. Kaieteur Falls is one of the most spectacular cataracts in the world and is the main geological feature of the national

park. The park was established in 1929 and encompassed 44 km^2 to protect the area around the falls, the Potaro gorge, and the surrounding Potaro Plateau. Today the park has been expanded to 627 km^2 to protect a greater representation of the vegetation around the falls and a larger expanse of the savannas and forests of the plateau. In 1998, the park was incorporated into the National Protected Areas System (NPAS) that is currently being developed as part of Guyana's ecotourism business. With this NPAS Project, Guyana urgently needs information on the biodiversity of the area before any conservation or management policy can be implemented. Botanical exploration of the mid- to lower portions of the drainage has been limited to the area around the falls and along the Potaro gorge; such exploration has resulted in a checklist of the vascular plants of the area (Kelloff & Funk 1998), but there have been virtually no ecological studies in an attempt to quantify species diversity.

In general, tropical forests have been characterized as having a high diversity of trees, with some inventories recording over 300 species with a diameter at breast height (DBH) ≥ 10 cm per hectare (Gentry 1988; Hubbell & Foster 1986; Valencia et al. 1994). Several hypotheses offer explanations regarding the maintenance of high diversity. Huston's (1979, 1994) "dynamic equilibrium hypothesis" suggests that diversity in populations is reached by low rate of competitive displacements or by periodic reductions in species (Huston 1979). If the population has a high number or high frequency of disturbances, slow-growing species will disappear and be replaced by the faster-growing pioneer species over time thus reducing diversity. In order to overcome this species must have some minimum growth rate to recover from population reductions. In other words, an increase in growth rates during periods of high frequencies of population reduction can actually increase diversity (Huston 1979). Another hypothesis is an ecological response to environmental conditions such as low and high light conditions. By changing the availability of resources, disturbances such as canopy gaps may influence succession. Those species efficient in recruitment quickly move in, and the site becomes covered with pioneer species (Bazzaz & Picket 1979). The ability to survive under low light conditions and the ability to achieve high growth under high light conditions is the most significant difference between species diversity (Bazzaz & Picket 1979; Hubbell 1995). It's the survival of the fittest that can utilize the disturbance, increasing the diversity of species. In Guyana, *Dicymbe* Spruce ex Benth., which is locally known as clump wallaba, produces coppices (suckers) on the healthy parent tree. When the parent trees die, these young trees can take advantage of the mature root system of the parent, as well as the light gap, and thus can out-compete other species in the area (Henkel 2003; ter Steege et al. 1993).

Not all tropical forests show a high alpha tree diversity, however. Productivity and disturbance vary in the tropics (Richards 1952; Connell & Lowman 1989), and this is evident in the mixed forests of central Guyana where there is a tendency for some species to dominate the vegetation (Davis & Richards 1934; Fanshawe 1952; Johnston & Gillman 1995; ter Steege 1993). Several examples of this type of forest in Guyana are the wallaba (*Eperua* Aubl.), mora (*Mora* Benth.), or clump wallaba (*Dicymbe*) forests (Davis & Richards 1934; Fanshawe 1954; Henkel 2003; ter Steege 2000b). These forests have a few species that represent a high percentage of the stems and/or basal area.

The tropical forest of Guyana contains a wide array of forest types, e.g., mangrove, moist and dry evergreen, montane, seasonal, swamp, and Greenheart forests. In swamp and mangrove forests, edaphic factors such as flooding and soil clearly explain these forest types (Fanshawe 1952). However, in the mixed forests of Guyana, the relationship between soil, hydrology, and forest types is not clear (ter Steege et al. 1993). Generally, classification of forest types has largely been based on climate, soil, and physiognomy (Ducke & Black 1954; Prance 1987), which reference species compositions or have generalized tropical floras at the genus or family level (Forero & Gentry 1988; Maguire 1970; ter Steege et al. 2000a). Recent studies used plots to examine patterns of plant diversity, e.g., how species richness (Gentry 1988) or habitat diversity contributes to species diversity (ter Steege 1993; Sabatier et al. 1997; Tuomisto & Ruokolainen 1997). Plot studies produce data at the species level and can provide long-term information on growth, mortality, regeneration, and dynamics of forest trees.

Sampling riparian trees of the plateau using a grid system of collecting allows us to (1) describe the

Fig. 1. Kaieteur Falls, located along the Potaro River in Guyana, has a single drop of 226 m into the splash basin below.

relative abundance and distribution of the trees, (2) provide a framework by which the forest structure of Kaieteur can be compared to other known study sites, (3) help fill in the missing tree taxa in the checklist, and (4) provide a standard by which forest structure and composition can be measured.

This paper presents the results of the two, one-hectare (ha) inventories carried out on the Potaro Plateau within Kaieteur National Park. Tree data from two other plot studies were used as a comparison of the tree diversity at Kaieteur. Data from two one ha plots were borrowed from a lowland forest in Guyana near the town of Kwakwani (a Guiana Shield community) and two one ha portions of a 50 ha plot at Barro Colorado Island, Panama (non-Guiana Shield community). In general, plot data from the Guiana Shield and particularly the Potaro Plateau are scarce (ter Steege et al. 2000a). One ha plots allow for us to quantify the relationship between tree species as well as among tree species and add to the knowledge of the tree diversity of Potaro Plateau in Guyana. The ultimate goal of this project was to document the species diversity and tree composition of the Wallaba (*Eperua*)-mixed forests of the Potaro Plateau and to compare the tree species diversity of Kaieteur National Park to those of other plots.

METHODS

The study site.—Kaieteur National Park is a mosaic of habitats consisting of exposed sandstone, grass savanna, scrub, and riparian forests. The average air temperature for the year is 26.5°C (USDA 1974). The average rainfall for the northeast face of the Pakaraima escarpment is approximately 3750 mm per year (Fanshawe 1953). Two 1 ha plots were established in the Wallaba (*Eperua*)-mixed forest of the Potaro Plateau. The study was conducted between 1995 and 1998 with sites selected based on the surrounding vegetation. In both 1 ha plots, some level of previous human disturbance was found (e.g. several large trees were removed for the building of the guesthouse). The first plot (Fig. 2a) is located at the headwaters of the Korume Creek (5°10'42"N, 59°29'44"W). The lower portion of the first plot is seasonally inundated and includes a portion of the creek in which grew a few patches of *Thurnia sphaerocephala* (Rudge) Hook.f. Along the western side of the plot, the land gradually rises up the ravine towards Muri-Muri savanna. The second plot (Fig. 2b) was established in the upland forest of the plateau between the Korume Creek and Potaro River gorge (5°11'16"N, 59°28'52"W). The terrain is rocky with a slight downward slope towards the northeastern part of the trail. There is no evidence of seasonal flooding as in the first plot.

The soils from these two sites were not analyzed, but it was generally observed that they consisted of a course white sand of quartzite with very little peat. These shallow white sand areas of the Pakaraima Plateau (Fanshawe 1954) are associated with the peneplain of the interior of Guyana.

The plots in the lowland area of Guyana used for comparison are located near the town of Kwakwani at the Aroaima (bauxite) mining site on the Berbice River, 238 km up the Canje River from New Amsterdam (5°30'N, 58°W). Data for these plots were kindly provided by James Comiskey (Smithsonian Institution Man in the BioSphere Program). The average rainfall recorded for this area is 2400 mm per year. The land is low lying with swampy areas near the river. The sites for the plots were selected within the area designated as "south mine," a proposed area for future bauxite mining. In this area, the shallow layer of topsoil (averaging 1.5 meters in depth) covers ca. nine meters of bauxite that overlays 60 meters of volcanic rock. Both plots were irregular in shape, and the vegetation is classified as non-flooded tropical mixed forest (Comiskey et al. 1994). It was noted that the soil was composed of a mixture of sand and clay with high porosity and high drainage. The soils were not sampled (Comiskey et al. 1993).

The second set of plots were part of a 50 ha study site at Barro Colorado Island (BCI) located near the Panama Canal at the Smithsonian Tropical Research Institution's station (9°9'17"N, 79°50'53"W). This forest is classified as a rich, old growth tropical forest dominated by Bombacaceae and Leguminosae (Condit et al. 1996). The terrain on the island's summit is relatively level with a variance of 28 meters in elevation. The average rainfall for this area is about 2500 mm per year (Condit et al. 1996) with a mean annual temperature of 27°C. The soil at BCI is a clay-rich tropical soil with an organic matter content (Yavitt 2000). Data from two of the 50 1 ha plots (designated as Hec21 & Hec37) were selected and kindly provided by Richard Condit for this study.

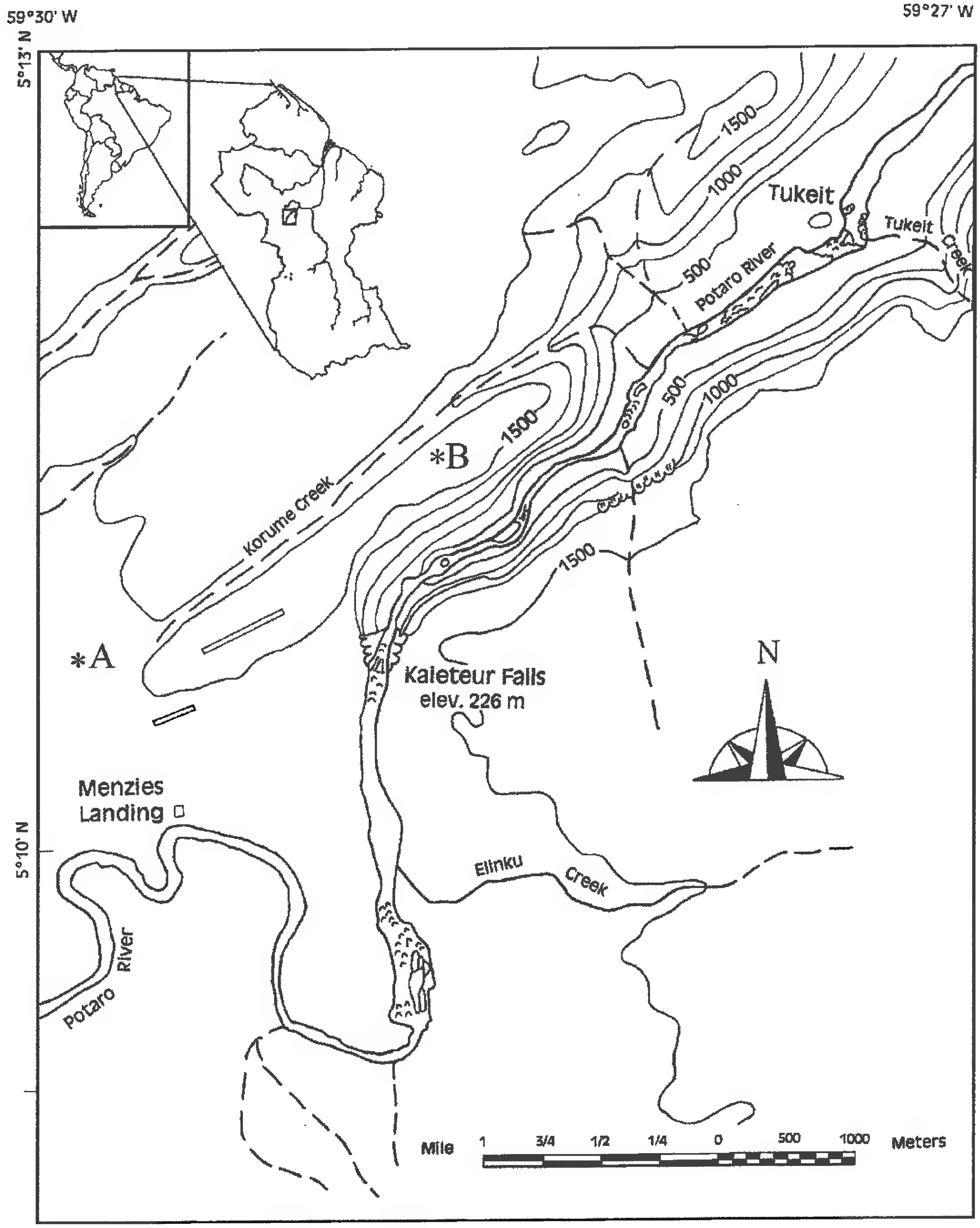

FIG. 2. Kaieteur National Park is located on the eastern portions of the Roraima formation. A. plot KF1 is located at the headwaters of the Korume Creek; B. plot KF2 is located near the Tukeit–Kaieteur trail on the plateau.

Established on the central plateau of BCI, the 50 ha permanent plot has a 70 year history of the flora and fauna and over 1500 scientific papers written on various topics (Hubbell & Foster 1992). For more information on Barro Colorado Island, selected readings are: Hubbell and Foster 1992 and Hubbell et al. 1995.

Census methods.—The method adapted for inventorying the woody vegetation of Kaieteur followed Dallmeier (1992). The terrain at both sites was uneven, and corrections were made to adjust for slope (Durr et al. 1988). The two 1 ha plots at Kaieteur were subdivided into 25 contiguous 20 × 20m quadrats, and all stems with a minimum DBH of 10 cm were measured. Spatial location of the trees within each quadrat was recorded for mapping purposes. Field vouchers were obtained, where possible, for each species encountered. Information was recorded to aid in identifications of the sterile vouchers, e.g.,features of the wood, bark, and sap (Polak 1992; Rosayro 1953). Romeo William, tree spotter and guide, assisted in the identifications of trees in the field. Local or vernacular names for trees (Fanshawe 1947, 1953, 1954) helped to identify morphologically similar trees. Most vouchers were sterile and thus required extensive time in the herbarium for identification. Trees were identified to the species level when possible, but were otherwise assigned to morphospecies.

Taxonomic nomenclature followed the "Checklist of the Plants of the Guianas: Guyana, Surinam, French Guiana" (Boggan et al. 1997). Voucher specimens were deposited in the Guyana National Herbarium, University of Guyana (BRG) and at the U.S. National Herbarium, Washington, DC (US).

Density, frequency, and dominance were calculated to describe how individual species are spatially distributed within the plot and how these distributions contribute to the community (Barbour et al. 1987). **Stem basal area (a)** and density of each tree were calculated using a = 0.7854 × (DBH) 2, where a = basal area of each tree in m^2 (Anderson & Ingram 1989). This measurement is useful in estimating canopy cover of trees because it assumes to take trunk **diameter at breast height (DBH)** into account. We also calculated **species basal area (BA)**, defined as the sum of all stem basal areas (a) of a given species. **Density** is defined as the number of trees per hectare, and **relative density** is the percentage of one species in relation to the total plant diversity. **Relative frequency** is expressed as a percentage of the number of quadrats that contain a given species. Dominance is an important ecological measurement. A species that contributes the most cover or basal area to the community is considered the dominant species. **Dominance** is calculated as the percent of basal area of a given species to total basal area (Balslev et al. 1987).

Finally, the relative contribution that a species provides to the community is called its importance value (Balslev et al. 1987). The **importance value index (IVI)** can be calculated by the addition of the relative density, frequency, and dominance for each species and for all trees at each site. High IVI values indicate that a species has a high basal area, frequency, and density at a site or when one or two of these parameters are much higher than other species (Felfili & da Silva 1993). The sum of relative parameters places species in a hierarchical order in the community and is useful for comparisons between different sites (Curtis & McIntosh 1951; Felfili & da Silva 1993). The IVI values can range from 0 to 300, with 300 representing a pure stand of one species (Balslev et al. 1987).

Statistical analyses.—Spatial and temporal variations in tropical tree communities can complicate the process of describing forest structure (Dutilleul 1993; Hall et al. 1998), and raw species data from plots can be too large and cumbersome to yield any meaningful intrinsic patterns. Ordination can reduce species abundance data into a space with fewer dimensions that can reflect sample configurations in ecological space (Gauch & Whittaker 1981). In community ecology, such ordinations can describe some of the strongest patterns in species composition (McCune & Mefford 1999; McCune & Grace 2002). Ecologists have applied metric ordination, which includes principal components analysis (PCA), to analyze vegetation data (Proctor 1967; Debinski & Brussard 1994; Tuomisto et al. 2003). This type of ordination assumes a linear relationship between the variables and is rarely amenable to ecological community data; it can also lead to considerable obscurity in data interpretations (Goodall 1953). Non-metric ordination methods are considered more powerful for analyzing vegetation data because this method assumes a non-linear relationship between the

variables and the use of ranked distances tends to linearize the relationship between the distances measured in environmental space and species space (McCune & Mefford 1999).

Species data per plot were summarized into data matrices (taxon vs. quadrat) and imported into PC-Ord (McCune & Grace 2002), a multivariant statistical program. Because the data represent quantitative scores per taxon, the original values were log transformed using $b_{ij} = \log(x_{ij} + 1)$, where the value of one is added to each species score to define zero values in the data. Log transformation reduces any dominant effects and normalizes the relative importance of common or rare species (Digby & Kempton 1987; McCune & Grace 2002). To visualize multivariate patterns among the quadrats, non-metric multidimensional scaling (NMS) was conducted using Sørensen (Bray-Curtis) distances for each plot and on each plot pair. NMS in PC-Ord is based on Mather's (1976) program and the algorithm of Kruskal (1964).

For each dataset in this study, the "autopilot" mode in PC-Ord was used. This mode provided a random starting configuration for each run. The program calculates each solution by running 40 runs with the real data and 50 runs with the randomized data, with a maximum number of 400 iterations for six axes. The program selected the best solution at each dimensionality where $p \leq 0.05$ for the Monte Carlo test and where that value of the "stress" parameter was the smallest number. Clarke's (1993) "rules of thumb" were used to interpret the final stress. Clarke found that most ecological community data will have values with a final stress between 10 and 20.

NMS provides an optimal ordination technique to analyze patterns in tree species composition for each of the studies. The final result in each analysis was an ordination in two-dimensional space. The two axes show the relationship between species abundance and the axis score.

RESULTS

Kaieteur National Park, Guyana.—There were 1724 total number of stems ≥10 cm DBH at Kaieteur in the two study plots. These stems covered a total basal area of 66.34 m^2/ha. Plot KF1 at Kaieteur contained 757 stems per hectare, with most taxa represented by a single stem. *Dicymbe pharangophila* R.S. Cowan (swamp wallaba, Leguminosae–Caesal.) produced coppice shoots from the base of the trunk that resulted in 65 stems being measured and tagged from a total of 28 trees. This habit of producing multiple stems from the base was also noted by Whitton (1962) and Henkel (2003) of *Dicymbe corymbosa* Spruce ex Bentham, another "swamp wallaba" found on the Potaro Plateau. The largest diameter tree recorded for the site was *Ocotea* sp. (Lauraceae), with a DBH of 89 cm. Other species with a DBH > 60 cm were *Pouteria* cf. *cuspidata* (A. DC.) Baehni (Sapotaceae) and *Swartzia schomburgkii* Bentham (Leguminosae–Fab.). Sixty-four percent of the stems were under 20 cm in diameter, and only one percent of the trees reached over 60 cm DBH. The two species that had the highest Important Value Index (IVI) were *Chamaecrista adiantifolia* (Spruce ex Bentham) H.S. Irwin & Barneby var. *pteridophylla* (Sandwith) H.S. Irwin & Barneby (Caesal.; IVI=20.052) and *Eperua falcata* Aublet, (Caesal.; IVI=15.427). These two species were found throughout the plot and accounted for 13.4% of the stems. *Dicymbe pharangophila* (IVI=14.679), *Ormosia coutinnoi* Ducke (Fab.; IVI=10.109), *Dicymbe* sp. (IVI=10.027) and *Pouteria cuspidata* (IVI=10.442) ranked next in importance. These species accounted for 32% of total stems recorded for KF1.

The understory species were not recorded, but it was noted that two species of Marantaceae (*Ishnosiphon* sp. and *Monotagma spicatum* (Aublet) J.F. Macbride) dominated the lower wet areas of the plot. One species of Bromeliaceae (*Ananas parguazensis* L.A. Canargo & L.B. Smith) dominated the dryer soils of the plot. *Thurnia spherocephala* (Ridge) Hooker f. (Thurniaceae) was quite abundant and grew in the flowing waters of the creek.

The second plot (KF2) at Kaieteur had more stems (967) than the first plot. *Dicymbe pharangophila* was nearly absent from this plot. *Chamaecrista adiantifolia* var. *pteridophylla* (95 cm DBH) and *Swartzia schomburgkii* Bentham (Fab.; 92 cm DBH) were the largest trees recorded for the site, followed by *Elizabetha* sp. (Caesal.; 66 cm DBH) and *Pouteria cuspitata* (64 cm DBH). Stems 20 cm DBH or less accounted for 69.5%, whereas only 1.0% of the stems exceeded 60 cm in diameter. Several species ranked high in IVI: *Eperua*

falcata (IVI=20.048), *Chamaecrista adiantifolia* var. *pteridophylla* (19.486), *Ocotea* spp. (IVI=18.253), and *Swartzia schomburgkii* (IVI=17.404). When *Catostemma commune* Sandw. (Bombaceae; IVI =15.082), *Ormosia coutinnoi* (IVI=12.328), and *Eperua* spp. (IVI=15.702) are added, these species account for 40.3% of the total stems recorded for plot KF2. The understory species were not surveyed, but it was noted that *Ishnosiphon* sp. and *Monotagma spicatum* were somewhat evenly distributed in the plot. *Vriesea splendens* (Brongn.) Lem. (Bromeliaceae) was seen along with the spiny bromeliad (*Ananas parguazensis*) from the first plot but was not as abundant. A broad-leaf aroid grew on tree trunks, and a Rapateaceae (*Stegolepis ferruginea* Baker f.) dominated the understory at quadrat 14.

In both plots at Kaieteur, the Leguminosae had the highest number of individuals per site (815 stems or 47.3% of the plots) most of which were from the subfamily Caesalpiniodeae (607). In plot 1 Bombacaceae ranked as the second most abundant family across all quadrats with 64 stems. Bombaceae, in plot 2, had 77 stems but ranked third after Lauraceae (136 stems).

Kwakwani, Guyana.—There were a total of 995 stems ≥ 10 cm DBH at Kwakwani in the two plots, these with a total basal area of 52.13 m²/ha. Five hundred and seven stems were recorded from first plot (AR1) at Kwakwani. Only four trees had a second stem measuring over 10 cm DBH. The largest tree on the site was *Trymatococcus amazonicus* Poepp. & Endl. (Moraceae) at 91 cm DBH. *Eschweilera pedicellata* (Rich.) S.A. Mori (Lechythidaceae) represented 23% of the total stems (115 stems) in this plot and had an IVI of 33.425. The taxon with the next highest IVI (6.751) was *Aspidosperma excelsum* Benth. (Apocynaceae) followed by *Bocageopsis multiflora* (Mart.) R.E. Fr. (Annonaceae; 6.733), *Unonopsis rufescens* (Baill.) R.E. Fr. (Annonaceae; 6.190), *Swartzia schomburgkii* (Fab.; 5.116), *Prunus* sp. (Rosaceae; 3.857), and finally *Cordia sagotti* I.M. Johnst. (Boraginaceae; 3.795). These taxa represented 163 stems or 21% of the stems counted in the site. Sixty three percent of the stems were under 20 cm DBH and only 2% were over 60 cm DBH: *Eschweilera pedicellata* (Lecythidaceae; 88.2 cm), *Aspidosperma excelsum* (Apocynaceae; 85.9 cm), *Albizia niopoides* (Spruce ex Benth.) Burkart (Leguminosae–Mimos.; 83.5 cm), *Inga pezizifera* Benth. (Mimos.; 76 cm), and *Bocageopsis multiflora* (Mart.) R.E. Fr. (Annonaceae; 72.8 cm).

The second plot (AR2) at Kwakwani had only 491 trees of single recordable stems. *Aspidosperma excelsum* was the largest tree (91 cm) and *Eschweilera pedicellata* had the highest IVI value of 63.671 (138 stems, 28% of the total stems). Two other taxa significant were *Mora gonggrijpii* (Kleinhoonte) Sandw. (Caesal.; IVI=36.486) and *Aspidosperma excelsum* (IVI=15.600). *Inga acrocephala* Steud. (Mimos.), *Mora gonggrijpii*, *Swartzia polyphylla* DC. (Fab.), *Eschweilera pedicellata*, *Chrysophyllum sparciflorum* Klotzsch ex Miq. (Sapotaceae), and *Aspidosperma excelsum* represented the 3% of the total stems over 60 cm DBH. Fifty-six percent of the total stems were under 20 cm.

Lecythidaceae was the most abundant family at Kwakwani, with 254 stems documented for the two plots. Leguminosae was the second most abundant with 184 stems (107 of these were Caesalpinioids in site 2). Next in rank were the Annonaceae with 55 stems over all quadrats in AR1 and Boraginaceae (34 stems). In site 2 these families represented only 19 and 2 stems. Apocynaceae had more stems (26) in AR2 and ranked third in abundance across the plot. All other families had less stems.

Barro Colorado Island, Panama.—In the two 1 ha plots selected from the Barro Colorado Island (BCI) 50 ha plot, the total basal area of trees ≥ 10 cm was 57.153 m²/ha. Information provided for this study includes only data for the main stem on each plot. No data were available for multiple stems and thus these were excluded from this study. The first plot (designated as Hec21 at BCI) had 418 trees. The tree that had the largest diameter on the site was *Hura crepitans* L. (Euphorbiaceae; 102.1 cm DBH). Seventy-five percent of the trees had < 20 cm DBH. Two percent of trees had a DBH > 60 cm: *Brosimum alicastrum* Sw. (Moraceae; 88.5 cm); *Chrysophyllum cainito* L. (Sapotaceae; 88.5), *Jacaranda copaia* (Aubl.) D. Don (82 cm) and *Tabebuia guayacan* (Seem.) Hemsl. (Bignoniaceae; 82 cm); *Prioria copaifera*, (Caesal.; 82 cm); and *Luehea seemannii* Triana & Planch. (Tiliaceae; 76.8 cm). The dominant species for Hec21 were *Faramea occidentalis* (L.) A. Rich. (Rubiaceae; IVI = 18.644), *Trichilia tuberculata* (Triana & Planch.) C.DC. (Meliaceae; IVI = 23.870),

Prioria copaifera, (Caesal.; IVI = 17.581), and *Alseis blackiana* Hemsl. (Rubiaceae; IVI = 10.344). These taxa accounted for 139 trees or one-third of the entire tree census.

The second plot (designated as Hec37 at BCI) contained 447 recordable trees, 62.6% of which were ≤ 20 cm DBH. *Ceiba pentandra* (L.) Gaertn. (Bombacaceae) was the largest tree in the plot with a diameter of 209.5 cm DBH. Other species over 60 cm DBH were *Ficus costaricana* (Liebm.) Miq. (Moraceae; 138 cm), *Tachigali versicolor* Standl. & L.O. Williams (Caesal.; 109.1 cm), *Hura crepitans* (Euphorbiaceae; 99.4 cm), *Aspidosperma cruenta* Woodson (Apocynaceae; 89.0 cm), *Dendropanax arboreus* (L.) Decne. & Planch. (Araliaceae; 83.0 cm), *Brosimum alicastrum* Sw. (Moraceae; 75.3 cm), and *Cecropia insignis* Liebm. (Cecropiaceae; 66.0 cm); *Guapira standleyana* Woodson (Nyctaginaceae; 75.3 cm); *Quararibea asterolepis* Pittier (Bombacaceae; 69.8 cm); and *Guatteria dumetorum* R.E. Fr. (Annonaceae; 63.5 cm). The dominant species on the site were *Faramea occidentalis* (IVI = 23.340) and *Trichilia tuberculata* (IVI=27.239); together, these two accounted for almost 31% of the total countable stems. Other species with high IVI values were two Bombacaceae: *Quararibea asterolepis* (IVI=14.721) and *Ceiba pentandra* (IVI=12.455).

From the two plots examined at Barro Colorado Island, Rubiaceae ranked the highest for individual stems (217). Meliaceae, with 122 trees, ranked second in the "tree per family" category. The Leguminosae contained only 67 stems, 47 of which were Caesalpinioids.

A comparative summary of the most abundant tree species from the six study sites can be found in Table 1.

Statistical analyses.—Non-metric multidimensional scaling (NMS) was used to reduce the datasets at each of the three study sites. In each plot there were several species that exhibited a strong relationship with the ordination scores. These species were displayed on the ordination as a joint plot. The radiating lines of the joint plot reflect the direction and strength of that species that is influencing the separation of the quadrats in the plot. Plot KF1 at Kaieteur had 103 species in the analyses. The final stress was 15.68692 for the 3-D solution with 99 iterations. The Monte Carlo test for this solution was $p \leq 0.0196$. The first two axes accounted for 56.8% of the variance; the first three accounted for 74.1%. Three patterns are seen in the grouping of quadrats based on species assemblages (Fig. 3A). *Dicymbe* spp., *Chamaecrista adiantifolia* var. *pteridophylla*, *Pachira flaviflora* (Pulle) Fern. Alnso. (Bombacaceae) form one group, and *Chamaecrista apoucouita* (Aubl.) H.S. Irwin & Barneby (Caesal.) and *Pterocarpus rohrii* Vahl (Fab.) form a second group; these two groups have a stronger influence in some of the quadrats whereas a third group composed of *Hevea guianensis* Aubl. (Euphorbiaceae), *Inga gracilifolia* Ducke (Mimos.) and species in Meliaceae have a stronger influence on others.

Kaieteur plot KF2 had the fewest species (71) in the dataset. The best result for the dataset is the 3-D ordination from NMS with a stress value of 13.30984 with 162 iterations (Monte Carlo $p \leq 0.0196$). The variance for the first two axes accounted for 66.4% of the variance; if the third axis is included, 82.5% of the variance is accounted for. Quadrats in the plot are separated into species assemblages influenced by two groups: the *Licania alba* (Bernoulli) Cuatrec. (Chrysobalanaceae), Bombacaceae spp., *Clathrotropis macrocarpa* Ducke (Fab.), *Eschweilara* spp., *Ocotea* spp., and *Macrolobium suaveolens* Spruce ex Benth. (Caesal.) group; and the *Henrettea ramiflora* (Sw.) DC. (Melastomataceae), *Sextonia rubra* (Mez) van der Werff (Lauraceae), *Inga* sp.3, and *Catostemma commune* Sandw. (Bombacaceae) in the other (Fig. 3B).

Combining the data from the two plots at Kaieteur, the best result from multiple NMS runs was a 3-D solution (stress = 18.09208, $p \leq 0.0195$) with a variance for the first two axes accounting for 54.6% or 75.0% including the third. The first two axes were chosen for the ordination to best represent the data (Fig. 3C). Axis 1 represents the area of collection and showed little separation between the locations of the plots. Axis 2 represents a clear separation between the species and their assemblages at plots KF1 and KF2. Species that contributed to the discrimination in KF1 were *Dicymbe pharangophila*, *Eperua rubiginosa* Miq. (Caesal.), and *Catostemma fragrans* Benth. (Bombacaceae). Species contributing to discrimination in KF2 were *Eperua* spp., *Sextonia rubra*, *Henriettea ramiflora*, and *Ocotea* spp. There was no overlap in species composition between quadrats of these two plots.

Table 1. A comparative summary of the most abundant tree species from Kaieteur National Park and Kwakwani, Guyana, and Barro Colorado Island, Panama. BA = Basal Area; IVI = Importance Value Index. Taxa are sorted from highest to lowest IVI.

Family	Taxa	Total stems	Ave. trees/ (m)	BA (M) DBH	Relative density	Relative domin.	Relative freq.	IVI
Kaieteur plot KF1								
Caesalpiniodeae	*Chamaecrista adiantifolia* (Spruce ex Benth.) H.S. Irwin & Barneby var. *pteridophylla* (Sandwith) H.S. Irwin & Barneby	59/61	0.201	2.306	8.613	7.186	4.253	20.052
Caesalpiniodeae	*Eperua falcata* Aubl.	40/40	0.221	1.788	5.839	5.571	4.017	15.427
Caesalpiniodeae	*Dicymbe pharangophila* R.S. Cowan	20/52	0.237	2.864	2.920	8.924	2.835	14.679
Sapotaceae	*Pouteria* cf. *cuspidata* (A. DC.) Baehni	20/24	0.249	1.580	2.920	4.923	2.599	10.442
Fabiodeae	*Ormosia coutinnoi* Ducke	23/23	0.246	1.333	3.358	4.153	2.599	10.109
Caesalpiniodeae	*Dicymbe* sp.	29/42	0.162	0.950	4.233	2.958	2.835	10.027
Caesalpiniodeae	*Eperua* sp.	22/24	0.221	1.175	3.212	3.661	3.071	9.944
Caesalpiniodeae	*Eperua rubiginosa* Miq.	21/21	0.191	0.770	3.066	2.398	3.308	8.771
Bombacaceae	*Pachira flaviflora* (Pulle) Fern. Alonso)	29/30	0.149	0.600	4.233	1.870	2.363	8.466
Fabiodeae	*Clathrotropis macrocarpa* Ducke	20/20	0.185	0.623	2.920	1.942	2.835	7.697
Leguminosae	Leguminosae sp.	15/18	0.230	0.932	2.190	2.903	2.363	7.455
Euphorbiaceae	*Hevea guianensis* Aubl.	18/20	0.207	0.938	2.628	2.922	1.654	7.204
Fabiodeae	*Pterocarpus* cf. *rohrii* Vahl	16/16	0.200	0.626	2.336	1.950	2.126	6.412
Fabiodeae	*Swartzia schomburgkii* Benth.	11/11	0.233	0.710	1.606	2.211	2.126	5.944
Caesalpiniodeae	*Chamaecrista apoucouita* (Aubl.) H.S. Irwin & Barneby	15/20	0.155	0.420	2.190	1.310	2.363	5.862
Bombacaceae	*Catostemma* cf. *fragrans* Benth.	17/17	0.157	0.355	2.482	1.106	2.216	5.714
Caesalpiniodeae	*Eperua grandiflora* (Aubl.) Benth.	13/13	0.228	0.667	1.898	2.079	1.181	5.158
Meliaceae	Meliaceae sp. 1	8/8	0.312	0.845	1.168	2.632	1.181	4.981
Mimosoideae	*Elizabetha* sp.	5/5	0.447	0.990	0.730	3.085	0.709	4.524
Lecythidaceae	*Eschweilera* ssp.	9/10	0.205	0.444	1.314	1.383	1.654	4.351
Bombacaceae	*Catostemma commune* Sandwith	11/11	0.162	0.251	1.606	0.781	1.890	4.277
Kaieteur plot KF2								
Caesalpiniodeae	*Eperua falcata* Aubl.	54/60	0.209	3.318	6.013	9.687	4.348	20.048
Caesalpiniodeae	*Chamaecrista adiantifolia* (Spruce ex Benth.) H.S. Irwin & Barneby var. *pteridophylla* (Sandwith) H.S. Irwin & Barneby	51/58	0.226	3.091	5.679	9.024	4.783	19.486
Lauraceae	*Ocotea* spp.	74/75	0.166	1.791	8.240	5.231	4.783	18.253
Fabiodeae	*Swartzia schomburgkii* Benth.	50/53	0.219	2.714	5.568	7.924	3.913	17.404
Caesalpiniodeae	*Eperua* sp.	54/59	0.169	1.680	6.013	4.907	4.783	15.702
Bombacaceae	*Catostemma commune* Sandwith	54/57	0.193	2.064	6.013	6.026	3.043	15.082
Fabiodeae	*Ormosia coutinnoi* Ducke	28/28	0.267	1.889	3.118	5.515	3.696	12.328
Caesalpiniodeae	*Chamaecrista apoucouita* (Aubl.) H.S. Irwin & Barneby	35/37	0.151	0.727	3.897	2.122	3.913	9.932

TABLE 1. continued

Family	Taxa	Total stems	Ave. trees/ (m)	BA (M) DBH	Relative density	Relative domin.	Relative freq.	IVI
Clusiaceae	Clusiaceae sp.	43/43	0.142	0.716	4.788	2.091	3.043	9.922
Melastomataceae	*Henriettea ramiflora* (Sw.) DC.	37/40	0.167	0.942	4.120	2.750	3.043	9.914
Fabiodeae	*Swartzia leiocalycina* Benth.	28/28	0.168	0.739	3.118	2.157	3.696	8.971
Caesalpiniodeae	*Clathrotropis macrocarpa* Ducke	29/30	0.171	0.856	3.229	2.501	3.043	8.773
Anacardiaceae	*Tapirira* sp.	15/15	0.273	1.475	1.670	4.308	2.391	8.369
Lauraceae	Ocotea rubra *Mez*	27/29	0.163	0.649	3.006	1.895	3.261	8.162
Caesalpiniodeae	*Macrolobium suaveolens* Spruce ex Benth.	21/26	0.206	0.999	2.338	2.917	1.957	7.212
Lecythidaceae	*Eschweilera* ssp.	22/25	0.163	0.548	2.450	1.599	3.043	7.092
Annonaceae	*Guatteria* sp.	18/18	0.161	0.412	2.004	1.203	2.826	6.033
Apocynaceae	*Aspidosperma excelsa* Benth.	17/18	0.139	0.287	1.893	0.838	1.957	4.687
Kwakwani plot AR1								
Lecythidacaeae	*Eschweilera pedicellata* (Rich.) S.A. Mori	114/115	23.9	7.400	22.619	31.068	2.131	55.818
Annonaceae	*Unonopsis rufescens* (Baill.) R.E. Fr.	29/29	21.6	1.249	5.754	5.244	0.888	11.886
Apocynaceae	*Aspidosperma excelsum* Benth.	26/26	25.3	1.363	5.159	5.722	0.977	11.858
Annonaceae	*Bocageopsis multiflora* (Mart.) R.E. Fr.	21/21	23.7	1.361	4.167	5.714	0.977	10.858
Boraginaceae	*Cordia sagotii* I.M. Johnst.	33/33	15.9	0.677	6.548	2.842	0.888	10.278
Fabiodeae	*Swartzia schomburgkii* Benth.	24/24	22.2	1.186	4.762	4.979	0.089	9.830
Rosaceae	*Prunus* sp.	30/30	15	0.566	5.952	2.376	1.421	9.749
Moraceae	*Pourouma cucura* Standl. & Cuatrec.	13/13	24.1	0.763	2.579	3.203	0.888	6.662
Anacardiaceae	*Tapirira guianensis* Aubl.	15/15	20.4	0.604	2.976	2.536	0.888	6.400
Celastraceae	*Goupia glabra* Aubl.	13/14	21.6	0.517	2.579	2.171	0.444	5.194
Fabiodeae	*Clathrotropis brachypetala* (Tul.) Kleinhoonte	14/14	14.2	0.242	2.778	1.016	0.888	4.682
Kwakwani plot AR2								
Lecythidaceae	*Eschweilera pedicellata* (Rich.) S.A. Mori	138/138	26.8	9.289	28.106	33.045	2.520	63.671
Caesalpiniodeae	*Mora gonggrijpii* (Kleinhoonte) Sandwith	80/80	23.3	5.166	16.293	18.378	1.815	36.486
Apocynaceae	*Aspidosperma excelsum* Benth.	26/26	26.7	2.500	5.295	8.894	1.411	15.600
Chrysobalanaceae	*Couepia guianensis* Aubl.	14/14	33.3	1.535	2.851	5.461	1.008	9.320
Sapotaceae	*Chrysophyllum sparsiflorum* Klotzsch ex Miq.	12/12	28.3	1.039	2.444	3.696	0.807	6.947
Fabiodeae	*Swartzia schomburgkii* Benth.	18/18	19	0.644	3.666	2.291	0.907	6.864
Lauraceae	*Chlorocardium rodiaei* (R.H. Schomb.) Rohwer, H.G. Richt. & van der Werff	15/15	22.3	0.647	3.055	2.302	1.008	6.365
Fabiodeae	*Swartzia polyphylla* DC.	8/8	33.8	1.023	1.629	3.639	0.807	6.075
Violaceae	*Paypayrola longifolia* Tul.	19/19	11.6	0.209	3.870	0.744	1.311	5.925
Myristicaceae	*Iryanthera juruensis* Warb.	17/17	13.2	0.246	3.462	0.875	1.109	5.446
Rosaceae	*Prunus* sp.	11/11	18.7	0.345	2.240	1.227	0.706	4.173

Table 1. continued

Family	Taxa	Total stems	Ave. trees/ (m)	BA (M) DBH	Relative density	Relative domin.	Relative freq.	IVI
Barro Colorado Island: Hec21*								
Meliaceae	*Trichilia tuberculata* (Triana & Planch.) C.DC.	42	26.5	2.742	10.048	12.319	1.503	23.870
Rubiaceae	*Faramea occidentalis* (L.) A.Rich.	58	12.0	0.671	13.876	3.015	1.753	18.644
Caesalpiniodeae	*Prioria copaifera* Griseb.	17	34.6	2.785	4.067	12.512	1.002	17.581
Rubiaceae	*Alseis blackiana* Hemsl.	22	20.6	0.908	5.263	4.079	1.002	10.344
Moraceae	*Brosimum alicastrum* Sw.	8	38.1	1.415	1.914	6.357	0.501	8.772
Arecaceae	*Oenocarpus mapora* H. Karst.	24	11.1	0.230	5.742	1.033	1.169	7.944
Bombacaceae	*Quararibea asterolepis* Pittier	11	27.8	0.856	2.632	3.846	0.918	7.396
Bignoniaceae	*Jacaranda copaia* D. Don.	6	43.7	1.177	1.435	5.290	0.417	7.142
Burseraceae	*Tetragastris panamensis* Kuntze	9	25.3	0.880	2.153	3.953	0.584	6.690
Apocynaceae	*Tabernaemontana arborea* Rose	10	26.7	0.701	2.392	3.149	0.668	6.209
Lecythidaceae	*Gustavia superba* O. Berg	9	27.1	0.549	2.153	2.466	0.751	5.370
Euphorbiaceae	*Hura crepitans* L.	2	61.1	0.850	0.479	3.819	0.167	4.465
Tiliaceae	*Apeiba aspera* Aubl.	7	26.4	0.506	1.675	2.273	0.417	4.365
Rubiaceae	*Randia armata* DC.	11	12.7	0.146	2.632	0.656	0.835	4.123
Barro Colorado Island: Hec37*								
Meliaceae	*Trichilia tuberculata* C. DC.	59	25.2	3.748	12.369	13.209	1.661	27.239
Rubiaceae	*Faramea occidentalis* (L.) A. Rich.	80	12.3	0.979	17.897	3.450	1.993	23.340
Rubiaceae	*Alseis blackiana* Hemsl.	25	29.5	2.108	5.593	9.422	1.329	16.344
Bombacaceae	*Quararibea asterolepis* Pittier	20	36.3	2.601	4.474	9.167	1.080	14.721
Bombacaceae	*Ceiba pentandra* (L.) Gaertn.	1	209.5	3.447	0.224	12.148	0.083	12.455
Olacaceae	*Heisteria concinna* Standl.	15	17.9	0.415	3.356	1.463	0.831	5.650
Moraceae	*Ficus costaricana* Miq.	1	138.0	1.496	0.224	5.272	0.083	5.579
Myristicaceae	*Virola sebifera* Aubl.	11	23.1	0.519	2.461	1.829	0.831	5.121
Meliaceae	*Guarea guidonia* (L.) Sleumer	12	19.8	0.422	2.685	1.487	0.831	5.003
Lecythidaceae	*Gustavia superba* O. Berg	11	21.0	0.403	2.461	1.420	0.748	4.629
Moraceae	*Brosimum alicastrum* Sw.	8	23.5	6.629	1.790	2.217	0.581	4.588
Nyctaginaceae	*Guapira standleyana* Woodson	5	41.3	0.803	1.119	2.830	0.415	4.364
Euphorbiaceae	*Drypetes standleyi* G.L. Webster	12	15.4	0.240	2.685	0.846	0.831	4.362
Cecropiaceae	*Cecropia insignis* Liebm.	6	36.1	0.730	1.342	2.573	0.415	4.330
Fabiodeae	*Swartzia simplex* Spreng. var. *grandiflora* (Raddi) R.S. Cowan	10	21.7	0.394	2.237	1.389	0.581	4.207
Burseraceae	*Protium tenuifolium* Engl.	10	19.3	0.328	2.237	1.156	0.664	4.057

*** Total stems not provided for Barro Colorado Island**

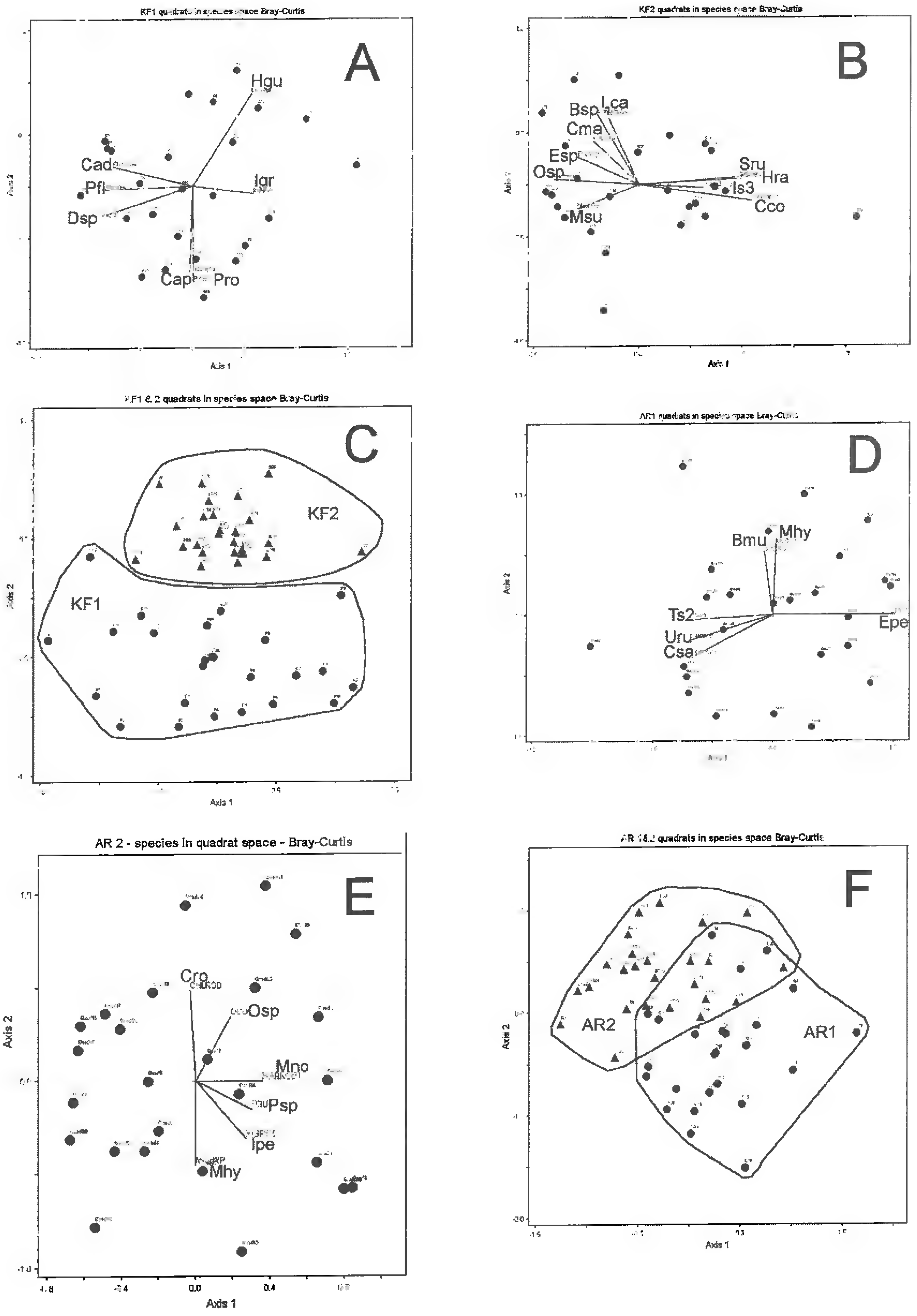

FIG. 3. Non-metric multidimensional scaling (NMS) ordination analyses of (A) Kaieteur, KF1, resulted in some degree of separation between three groups based on species assemblages dominated by: *Dicymbe* spp. [Dsp], *Chamaecrista adiantifolia* var. *pteridophylla* [Cad], *Pachira flaviflora* [Pfl] in one group, *Chamaecrista apoucouita* [Cap] and *Pterocarpus rohrii* [Pro] in the second and *Hevea guianensis* [Hgu] and *Inga gracilifolia* [Igr] in the third; (B) the quadrats of Kaieteur, KF2, separate into two groups with species assemblages of *Licania alba* [Lal], Bombacaceae spp. [Bsp], *Clathrotropis macrocarpa* [Cma], *Eschweilara* ssp. [Esp], *Ocotea* spp. [Osp], and *Macrolobium suaveolens* [Msu] in one group and *Henrettea ramiflora* [Hra], *Sextonia rubra* [Sru], *Inga* sp.3 [Is3], and *Catostemma commune* [Cco] in the other group; (C) combined species data from both plots [KF1 & KF2] at Kaieteur indicate little to no overlap in species assemblages between the quadrats; (D) ordination of tree species at Kwakwani, AR1, with quadrats separating into three groups based on analyses; these groups were dominated by: *Unonopsis rufescens* [Uru], *Cordia sagotii* [Csa], *Tapirira* sp.2 [Ts2] in one group, *Miconia hypoleuca* [Mhy], *Bocageopsis multiflora* [Bmu] in the second, and *Eschweilera pedicellata* [Epe] as the only species in the third; (E) at the second plot at Kwakwani, AR2, *Eschweilera pedicellata* and *Mora gonggrijpii* significantly outweighed the other species and were removed from the calculations. The subdominant species that influenced the groupings were *Miconia hypoleuca* [Mhy], *Inga pezizifera* [Ipe], *Prunus* sp. [Psp], *Chlorocardium rodiaei* [Cro], *Margaritaria nobilis* [Mno] and *Ocotea* spp. [Osp]; (F) the combined species data from both plots [AR1 & AR2] at Kwakwani had an overlap of approx. 50% of the quadrats between the study sites.

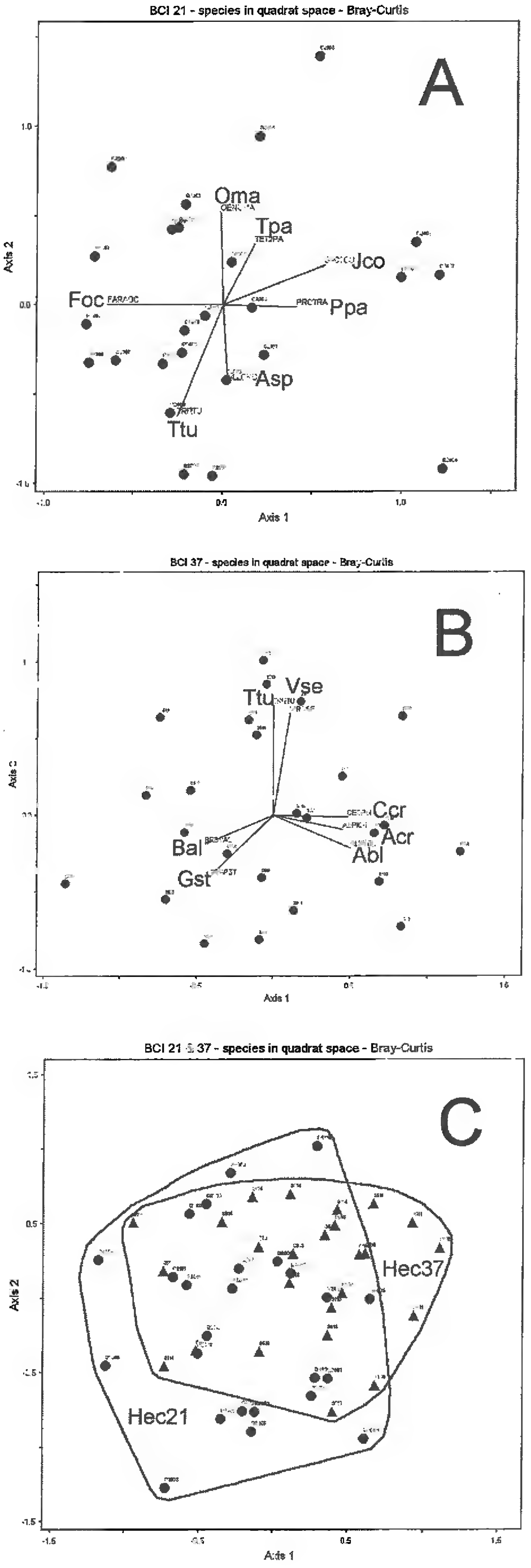

Fig. 4. Non-metric multidimensional scaling (NMS) ordination analyses for (A) Barro Colorado Island plot, HEC21, resulted in separation between three groups based on species assemblages dominated by: *Trichilia tuberculata* [Ttu] and *Allophylus psilospermus* [Aps] in the first group, *Protium panamense* [Ppa], *Jacaranda copaia* [Jco], *Tetragastris panamensis* [Tpa], and *Oenocarpus mapora* [Oma] in the second, and *Faramea occidentalis* [Foc] in the third; (B) the quaddrats of Barro Colorado Island HEC37, separated into three groups with species assemblages dominated by: *Trichilia tuberculata* [Ttu] and *Virola sebifera* [Vse] in the first group, *Cecropia insignis* [Cin], *Aspidosperma cruenta* [Acr], and *Alseis blackiana* [Abl] in the second, and finally, *Brosimum alicastrum* [Bal] and *Guapira standleyana* [Gst] in the third; (C) ordination of the 114 species in the combined dataset for Barro Colorado Island plots [Hec21 7 Hec37] indicates a similarity of species composition between the two sites.

Ordination was used to reduce the datasets at the Kwakwani study site. Site AR1 had 84 species with a final analysis in a 3-D solution of 15.71292 (stress) over 82 iterations ($p \leq 0.0196$). The overall patterns between the quadrats indicate some differences in species composition between the plots. The quadrats separated into several groups (Fig. 3D). These assemblages were defined by *Unonopsis rufescens* (Baill.) R.E. Fr. (Annonaceae), *Cordia sagotii* I.M. Johnst. (Boraginaceae), *Eschweilera pedicellata*, *Miconia hypoleuca* (Benth.) Triana (Melastomataceae), *Bocageopsis multiflora* (Mart.) R.E. Fr. (Annonaceae) and *Tapirira* sp.2 (Anacardiaceae). The first two axes accounted for 53.0% of the variance. Including the third, 72.9%of the variance was accounted for.

At site AR2, there were 58 species in the matrix. *Eschweilera pedicellata* and *Mora gonggrijpii* were abundant throughout the plot. Since their higher weight contributed more than the other species, NMS failed to find a useful ordination. *Eschweilera pedicellata* and *Mora gonggrijpii* were deleted for remaining calculations. The result was a 4-D solution (stress = 13.80266; $p \leq 0.0392$) for this plot (Fig. 3E). The first two axes accounted for 18.7%, and the third added only 34.6% of the variance. These assemblages were defined by the following species in the plot: *Miconia hypoleuca* (Benth.) Triana (Melastomataceae), *Inga pezizifera* Benth. (Mimos.), *Prunus* sp. (Rosaceae), *Chlorocardium rodiei* (R.H. Schomb.) Rohwer, H.G. Richt. & van der Werff (Lauraceae), *Ocotea* spp., and *Margaritaria nobilis* L.f. (Euphorbiaceae). Combining the datasets for both plots at Kwakwani resulted in 93 species in the analysis. NMS ordination yielded a 3-D solution with a stress of 19.64717 ($p \leq 0.0196$) over 326 iterations. The first two axes accounted for 44.1% of the variance (65.7% with all three). Fifty percent of the quadrats from both plots had species compositions that were similar. *Swartzia schombergkii*, *Prunus* sp., *Mora gonggrijpii*, *Couepia guianensis* Aubl. (Chrysobalanaceae), and *Aspidosperma excelsum* were the species that define the assemblages in the BCI plots. *Eschweilera pedicelliata* was abundant in both plots (Fig. 3F).

At the Barro Colorado Island (BCI) Hec21 plot, a total of 92 species was observed. The final stress for the 3-D solution was 15.82730 ($p \leq 0.0196$) in 88 iterations. The first two axes accounted for 49.2% of the variance (73.8% with all three). Figure 4A shows the result of the non-metric scaling. The angle and length of the radiating lines in the joint plot indicate the direction and strength that each species has with the ordination score. Radiating vectors indicated that *Trichilia tuberculata*, *Allophylus psilospermus* Radlk. (Sapindaceae), *Protium panamense* (Rose) I.M. Johnst. (Burseraceae), *Faramea occidentalis*, *Jacaranda copaia*, *Tetragastris panamensis* Kuntze (Burseraceae), and *Oenocarpus mapora* Karst. (Arecaceae) had the strongest relationship with the ordination scores.

The BCI plot Hec37 had 82 species; the ordination had a final stress of 17.47696 over 131 iterations ($p \leq 0.0392$). The first two axes accounted for 30.5% of the variance and the first three, 61.1% of variance. The species that contributed to discrimination in this plot were *Trichilia tuberculata*, *Virola sebifera* Aubl. (Myristicaceae), *Cecropia insignis*, *Aspidosperma cruenta*, *Alseis blackiana*, *Brosimum alicastrum*, and *Guapira standleyana* (Fig. 4B).

A total of 114 species in the two BCI plots was observed. The resulting ordination of the combined plots produced a 3-dimensional solution with a stress of 21.77097 ($p \leq 0.0392$) in 400 iterations. The variance explained by the first two axes was 33.6% and 58.1% including the third. The quadrats of the two plots overlapped significantly, indicating a similarity of species composition within each plot (Fig. 4C). The species with the strongest relationship in this ordination were *Trichilia tuberculata*, *Adelia triloba* Hemsl. (Euphorbiaceae), *Oenocarpus mapora* and *Jacaranda copaia*.

DISCUSSION

Establishing two permanent biodiversity monitoring plots at Kaieteur National Park has provided Guyana with the scientific data required for the prioritization of conservation initiatives. This study provides baseline data on tropical woody plant communities to aid in measuring ecological change over time and to help distinguish between natural and human impact. Measuring relative density, relative frequency, relative dominance, and importance index values of individual species provides information on how species

are distributed within the forest and how they contribute to the community in which they live. Using a standardized methodology for surveying all trees ≥ 10 cm DBH ensures comparability with other study sites and provides a framework for studying the dynamics of tropical forests. This survey at Kaieteur resulted in 133 taxa representing 1586 trees (1,725 stems ≥ 10 cm in DBH) almost twice the number of trees from the Kwakwani, Guyana or Barro Colorado Island, Panama. The density of trees at Kaieteur were similar to a caatinga forest on white sand at Pico da Neblina in Brazil where 1569 trees were measured in two one-hectare plots (Boubli 2002). The number of stems recorded in each plot at Kaieteur bordered on the upper range of stems per hectare (965 stems ha^{-1}) found on similar plot studies. This high number of stems were found by Davis and Richards (1933, 1934) in five plots at Moraballi Creek, Guyana (460 to 919 trees per 122 x 122 m plot) where as those of similar studies in the Neotropics for trees ≥ 10 cm DBH have not been. Sabatier and Prévost (1990), Poncy et al. (1998), and Bordenave et al. (1998) found densities of 473 to 570 stems per hectare at Les Nouragues, French Guiana, and up to 882 stems per hectare in one particular transect (Sabatier & Prévost 1990). Johnston and Gillman (1995) recorded 357 to 742 trees per hectare at the four one-hectare study plots at Kurupukari, Guyana. At the El Caura Forest Reserve, South Venezuela, mean densities ranged from 563–573 trees ha^{-1} (Castellanos 1998). In Manaus, Brazil mean densities were 550 stems ha^{-1} (Ferreira & Rankin-de-Mérona 1998).

Davis and Richards (1934) noted that the forest at Moraballi Creek dominated by *Eperua falcata* had an extraordinary large number of trees ha^{-1} and that Leguminosae was the most abundant family (Whitton 1962). This was also noted by Boubli (2002) at Neblina where *Eperua leucantha* Benth. accounted for a large percentage of the stems. Guyana's rain forests can be dominated by one to several species, these often in the same family (Davis & Richards 1933; Fanshawe 1952; Whitton 1962; Henkel 2003). Kwakwani's plots were dominated by Lecythidaceae (30.9%) and Kaieteur's (47%) were dominated by Leguminosae. This is not unique to Guyana as a Lecythidaceae or Leguminosae dominance can be found in many other tropical forests, e.g., Richards 1952; Whitton 1962; ter Steege 1993; Nascimento & Proctor 1994; Henkel 2003.

Stem diameters were summarized into two categories (10 cm increments and percentage of stems per class size) in order to facilitate comparisons between the study sites (Table 2). The distribution of tree per class size in the six plots shows a characteristic inverse J-shape (Fig. 5) typical of forests that have been relatively undisturbed in the recent past (Lindeman & Mori 1989), with over 56% of the trees equal to or less than 20 cm DBH. Overall, the stem class size distributions from 20.1 cm to 60 cm DBH at Kaieteur were comparatively similar to Kwakwani and BCI in this paper. Total percentage of stems below the 40.1 cm DBH class in each of the three study sites ranged from a low of 86.7% at BCI to 95.9% at Kaieteur plot KF2. Boubli (2002) commented that 46% of trees at Neblina were small in girth while Whitton (1962) commented that in the Wallaba forests of Guyana, very few trees exceed 70 cm in diameter. At Kaieteur only ca. 2% reached the larger diameters with only three species, these all Caesalpinioid legumes, reaching over 30 cm DBH: *Eperua falcata*, *Chamaecrista adiantifolia* var. *pteridophylla* and *Swartzia schomburgkii*.

The total calculated basal area/ha from the three sites in this study ranged from 52 to 66 m^2 / ha. Kwakwani and BCI were similar to the 53 m^2/ha found by Whitton (1962) and Mori and Boom (1987) at Saül, French Guiana, but higher than those found in the forest plots (27–34 m^2/ha) of Central Amazonia (Rankin-de-Merona et al. 1992). Kaieteur's total basal area (66 m^2/ha) was similar to that of Neblina (Boubli 2002, 73 m^2/ha).

In order to understand the importance value index (IVI) of each species and how it contributes to the community one has to look at its relative parameters. Of all the Caesalpiniodeae legumes at Kaieteur two species, *Eperua falcata* and *Chamaecrista adiantifolia* var. *pteridophylla*, yielded a total IVI value of 75.0. These species were widely spread throughout the plots, had a more stems than other species. In the lowland area of Kwakwani, the highest IVI values (119.5) for both sites came from one species of Lecythidaceae, *Eschweilera pedicellata*. This species dominated the plots and was higher than the Lecythidaceae at La Fumée Mountain, French Guiana (Mori & Boom 1987). Such high IVI values have only been recorded elsewhere by Gibbs et al. (1980) for *Cyclolobium vecchii* A. Samp. ex Hoehne (Leguminosae; IVI=82) and *Sebastiania klotschiana*

TABLE 2. Stem class size in cm DBH (number of stems/percent of stems) at Kaieteur National Park and Kwakwani, Guyana, and Barro Colorado Island, Panama.

	≥ 10.0	≥ 20.1	≥ 30.1	≥ 40.1	≥ 50.1	≥ 60.1	
Kaieteur							
	Plot 1	488 / 64.3	147 / 19.4	72 / 9.5	28 / 3.7	15 / 2.0	8 / 1.0
	Plot 2	673 / 69.6	201 / 20.8	53 / 5.5	19 / 2.0	11 / 1.1	10 / 1.0
Kwakwani							
	Site 1	316 / 62.2	110 / 21.6	45 / 8.9	14 / 2.8	7 / 1.4	13 / 2.6
	Site 2	277 / 56.4	107 / 21.7	60 /12.2	20 / 4.1	12 / 2.4	15 / 3.1
Barro Colorado Island							
	Hec21	287 / 68.7	52 / 12.4	38 / 9.1	19 / 4.6	9 / 2.1	13 / 3.1
	Hec37	280 / 62.6	88 / 19.7	36 / 8.1	13 / 2.9	14 / 3.1	16 / 3.6

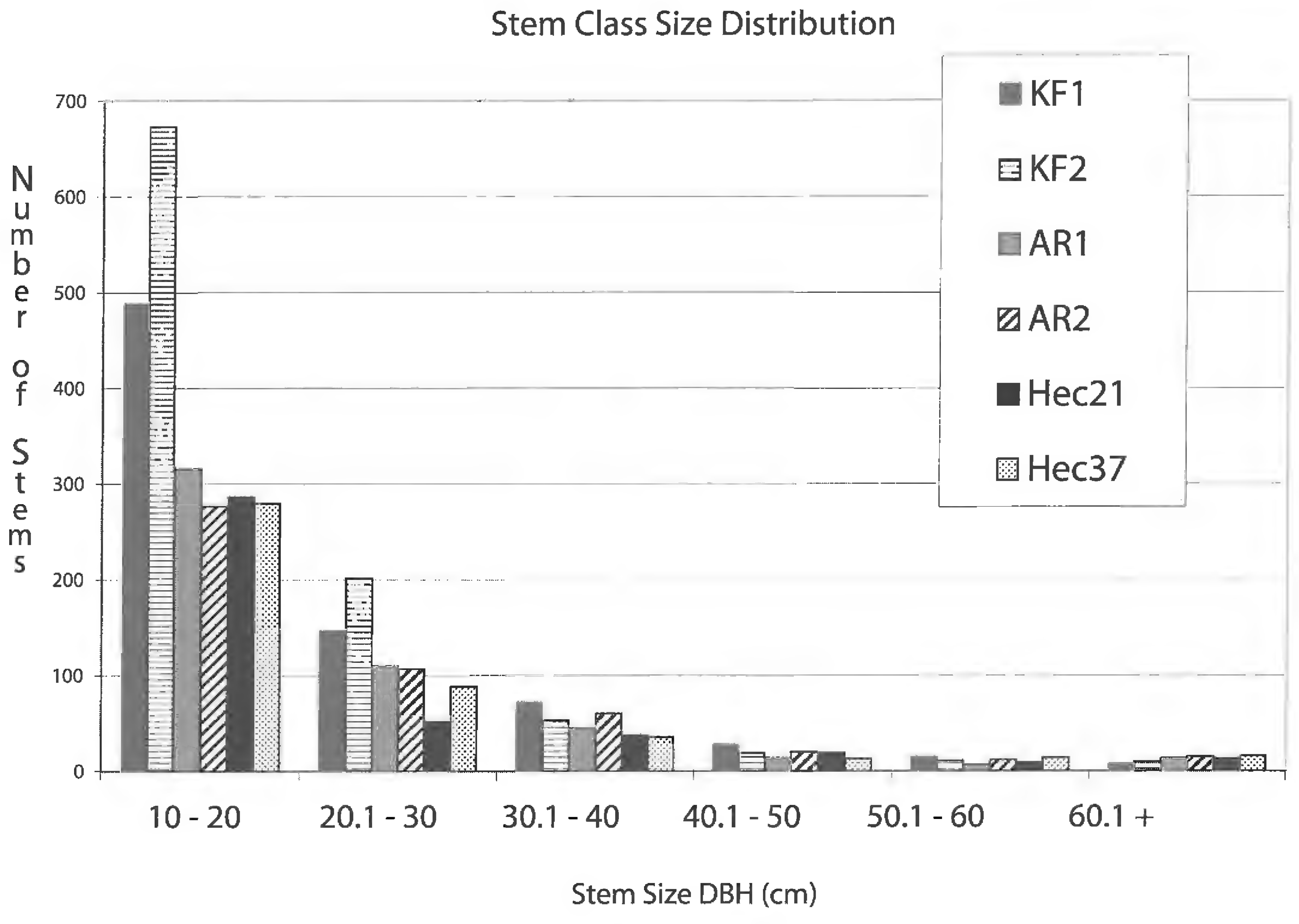

FIG. 5. Distribution of stem diameters in the six study plots of Kaieteur (KF), Kwakwani (AR) and Barro Colorado Island (Hec) shows the characteristic inverse J-shape typical of relatively undisturbed forests.

(Muell. Arg.) Muell. Arg. (Euphorbiaceae; IVI=119) from his survey in Mugi-Guiçu, Brazil. At Barro Colorado Island to species in different families scored high, *Trichilia tuberculata* (Meliaceae, IVI=51.1) and *Faramea occidentalis* (Rubiaceae, IVI=41.9).

When the plot data were examined at the family level, there were 33 families at Kaieteur and 36 at Kwakwani. The number of families in the Guyana plots was lower than the number of families recorded by Balslev et al. (1987) for the floodplain (44) and non-flooded forests (53) of Añangu, Ecuador. It was also lower than the 42 families at BCI. Thirty-three percent of the families were found in all three study sites, with

Table 3. Dominant families within the three sites with a combined total of over 50% of the stems: Kaieteur (KF), Kwakwani (AR), and Barro Colorado Island (BCI). Numbers shown are percentages of overall stems per family found at each site.

	KF	AR	BCI
Annonaceae	-	7.4	-
Apocynaceae	-	5.2	-
Arecaceae	-	-	5.6
Bombacaceae	8.2	-	-
Euphorbiaceae	-	-	4.3
Lauraceae	9.5	-	-
Lecythidaceae	-	25.4	-
Leguminosae	49.2	18.4	7.6
Meliaceae	-	-	14.1
Rosaceae	-	4.1	-
Rubiaceae	-	-	25.1

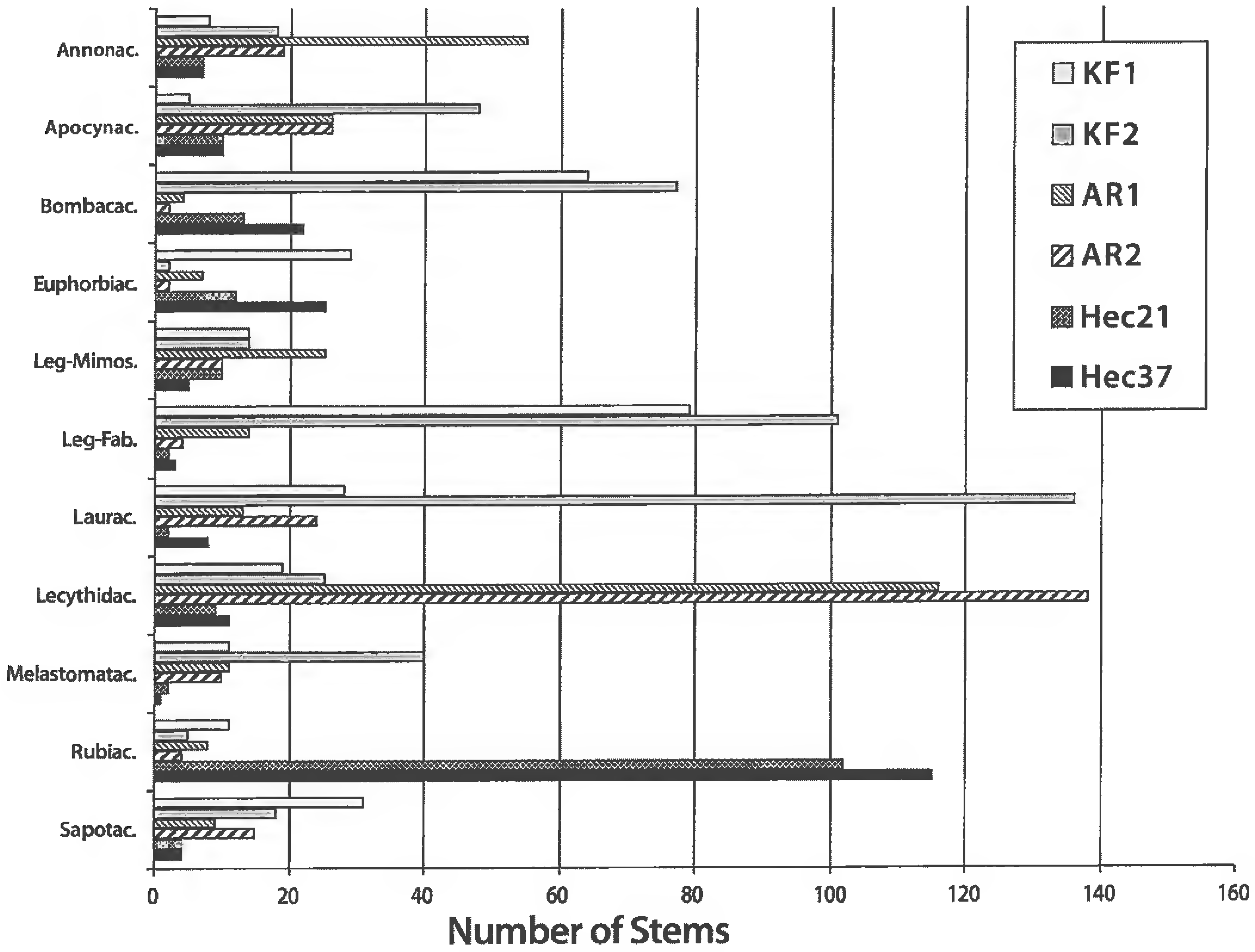

Fig. 6. Total number of stems for each family shared by Kaieteur and Kwakwani, Guyana and Barro Colorado Island, Panama (Caesalpinioideae dominated the plots at Kaieteur with over 300 stems/ha outweighing all other families so it was excluded from this figure.)

the dominant families varying among the sites (Table 3). The total number of stems for each family shared by all three sites is compared in Figure 6. Caesalpinioideae dominated the plots at Kaieteur with over 300 stems/ha. Subsequently, it was necessary to leave this subfamily of Leguminosae out of the comparison so that the bars on the graph representing families with less than 50 stems would be displayed.

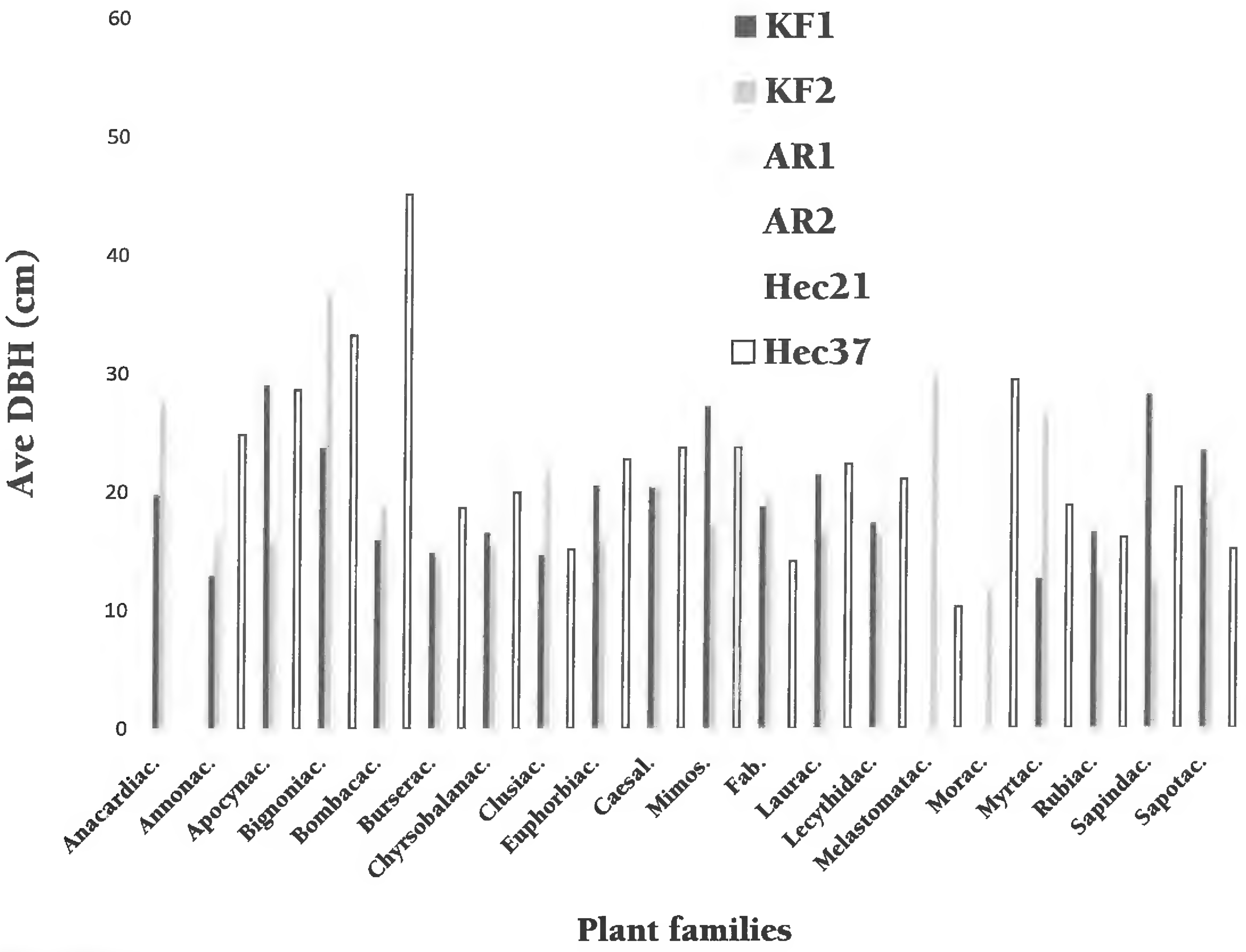

Fig. 7. Average diameter at breast height (DBH) of the major tree families at Kaieteur and Kwakwani, Guyana and Barro Colorado Island, Panama. Key to the abbreviations: KF1=Kaieteur, plot 1; KF2=Kaieteur, plot 2; AR1=Kwakwani, site 1; AR2=Kwakwani, site2; Hec21=Barro Colorado Island, plot 1; Hec37=Barro Colorado Island, plot 2.

When the average diameter at breast height of major tree families at Kaieteur, Kwakwani, and BCI were compared (Fig. 7), the DBH ranged from 10.2 cm (Melastomataceae) to 47.7 cm (Bombacaceae). The largest tree recorded among the research sites was an individual of *Ceiba pentandra*, Bombacaceae, from Hec37 at Barro Colorado Island, with a DBH of 209.5 cm.

From the 325 taxa recorded for the three study sites, only 3% (10 species) of all species were shared between the plots. *Apeiba aspera*, *Brosimum alicastrum*, and *Virola surinamensis* were shared between Barro Colorado Island and Kwakwani. *Catostemma fragrans*, *Licania alba*, *Swartzia schomburgkii*, and *Tapirira guianensis* were shared by Kwakwani and Kaieteur. BCI and Kaieteur shared only *Pterocarpus rohrii*. The only species shared by all three sites was *Jacaranda copaia*. Thus, there is a substantial lack of overlap in species composition among these tropical tree communities. Comparing genera among sites, only 6% were shared among Kaieteur, Kwakwani and Barro Colorado Island. These were *Aspidosperma*, *Inga*, *Jacaranda*, *Licania*, *Ocotea*, *Pouteria*, *Protium*, and *Swartzia*. When pair-wise comparisons were made between the sites, BCI and Kwakwani shared 8.1% of their genera. Kwakwani and Kaieteur Falls shared 6.3% and 5.0% was shared between BCI and Kaieteur. Based on a phytogeographical study of the taxa at Kaieteur, the flora of this area has its strongest affinity (42%) with the Guiana Shield area of South America with only about 15% of the taxa having a widespread distribution across the Neotropics (Kelloff & Funk 2004).

Statistically, non-metric (NMS) ordination on ecological data derived from PC-ORD has helped to describe the vegetation data from the plots at Kaieteur National Park and Kwakwani, Guyana and Barro

Colorado Island, Panama. In all six plots, the first two axes describe the relationship or dissimilarity between the quadrats (in ordinary space) and represent this variation in ordination space (McCune & Grace 2002). The quadrats with floristic similarities tend to form loose clusters. In the joint plots these similarities suggest trends that can be indicators of microhabitats induced by substrate characteristics, hydrology and/or other edaphic effects in the site. The Janzen-Connell model for tropical tree diversity proposes that seeds and seedlings in proximity of conspecific adults are have a higher mortality rate resulting in recruitments some distance from the parent tree leaving space for colonization by other species (Schupp 1992). Other factors to consider are the ability of the species to disperse its seeds, the competition for light or nutrients, pollinators.

Ordination of tree species at Kaieteur separated the 20 × 20 m quadrats in each plot primarily by species composition. The quadrats were strongly correlated with some of the less dominant tree species such as *Eperua rubiginosa, Inga gracilifolia, Bombax flaviflora, Dicymbe* sp., *Hevea guianensis* in KF1 and *Pouteria cuspidata, Clusia* sp., *Tapirira* sp., *Licania canella* and *Byrsonima incarnata* in KF2. Some species such as *Hevea guianensis* that grows along more inundated soils and *Bombax flaviflora* of the dryer soils may help explain the variation in the plots. Although the soils of the Potaro Plateau are largely composed of porous white sand with very little nutrients, slope, accumulation of leaf litter, and hydrology can change over relatively short distances (C. Kelloff, pers. obs.). Although dominated by *Eperua falcata* and *Chamaecrista adiantifolia* var. *pteridophylla*, the two plots at Kaieteur indicate differences in the forest community over very short distances (Fig. 5). This was not the case at Kwakwani or BCI where analyses indicated some overlap in species composition between the quadrats of the plot pairs at each study site.

Although a forest type may be designated based on the dominant species, the forest is not without an array of subdominant or even rare species that have an overall large effect on the floristic composition of the forest. Such changes can occur over distance and time with changes in light (tree falls), seed dispersal, soil composition or by turn-over (David & Richards 1934). An example of one such change is in the Kaburi district of Guyana where the *Eperua falcata* forests were replaced over time by *Dicymbe corymbosa* Spruce ex Benth. which expanded its dominance by self-pollarding, thus replacing mature trees with large clumps of slender stems (Davis & Richards 1934) and eventually crowding out the other species. The forest at Kaieteur could not be considered a monodominant stand nor could it be considered strictly a Wallaba (*Eperua*) forest. As seen in plot 2 *Chamaecrista adiantifolia* var. *pteridophylla* became the dominate species in that area of the forest. The main family that dominated the forest was the Caesalpiniodeae of the Leguminosae with over 300 stems. The subdominant families range from Lauraceae, Bombacaceae, Clusiaceae, and Fabiodeae.

CONCLUSION

Plots can be a powerful tool for providing long-term information on forest composition, diversity and structural change. They can then be used to assess changes in the forest over time, and the information gathered from plots can be used to understand how other physical parameters may influence species composition and distribution (Dallmeier & Comiskey 1998).

The two plots established at Kaieteur National Park were only a small sampling of the riparian forests of the Potaro Plateau. The information gathered on the tree composition of just one area on the plateau demonstrates the diversity and turnover in this forest. The Wallaba (*Eperua*)–mixed forest plot study at Kaieteur had a larger number of trees per unit area over 10 cm DBH and represented almost twice the stems surveyed in the Mora forests at Kwakwani, Guyana or in the lowlands of Barro Colorado Island, Panama. The plots at Kaieteur were similar to the white sand forest studies by Whitton (1962) at Amatuk, Guyana and by Boubli (2002) at Neblina, Brazil, with their large number of trees and dominance of the family Leguminosae. One hypothesis presented by Torti and Coley (1999) suggested that legumes may be more successful in this region because they have ectomycorrhizal fungi that are good scavengers for nutrients in the otherwise nutrient poor soils and that these fungi suppress saprophytic fungi that are potentially detrimental to this symbiosis. A study by ter Steege and Hammond (2001) suggested that seedlings were compensating for low

light conditions by providing an internal energy source in the form of large cotyledons. Bulky endosperms sustained larger seedlings and supported juvenile plants when light were insufficient. Although designated as a Wallaba-mixed forest, Kaieteur did not have a single dominant species such as *Eschweilera pedicellata* that was dominant in the lowland forest of Kwakwani. Studies have shown that Kaieteur has a strong affinity to the Guiana Shield flora (Kelloff & Funk 2004) with an upland element of the Roraima formation. This was noted from this study with via a similarity of Kaieteur to Pico da Neblina in Brazil.

Non-metric multidimensional scaling (NMS) methods for examining vegetation data from ecological communities are valuable tools for researchers. NMS examines the relationship between floristic dissimilarities of vegetation and subsequent ecological inference. Statistical analyses of the plots at Kaieteur National Park revealed dissimilarities in the species composition between the plot pairs. This suggests subtle changes in microhabitats and species dynamics of the subdominant tree taxa on the Potaro Plateau.

This study has shown that two 1 ha plots can adequately demonstrate how diverse tree species are in one section of the forest; furthermore, it indicates that sampling was probably too small to capture all of the different habitats represented at Kaieteur National Park. It still remains to be understood why the Caesalpiniodeae and in particular the *Eperua* and *Chamaecrista* dominated the forest. Does this indicate favorable ecological condition, the Janzen-Connell effects or can the Caesalpiniodeae legumes with its root nodules thrive better is the nutrient poor soil of the Potaro Plateau? To answer these questions more studies need to be done on the soils of the plateau.

Forests on white sand generally have a lower alpha-diversity than those on terra firme (ter Steege et al. 2000a) but noted for their monodominance and high abundance of several tree families, such as the Caesalpiniaceae. These forests also have trees that are locally abundant but globally restricted such as the Greenheart, *Chlorocardium rodiei* (Rob. Schomb.) Rohwer, Richter, & van der Werff (Lauraceae), in central Guyana. Development or poorly designed logging and mining practices can quickly lead to irreversible damages to the forests and habitats, with eventual species loss or extinction. Analysis of the diversity and the composition on the scale of plots can provide some of the best information needed define protected areas in Guyana (ter Steege et al. 2000b; Kelloff 2003). It is on this scale that we can best understand plant spatial distributions and how radically these can change over a relatively small geographic area.

The information collected in the plot study at Kaieteur National Park can be useful for monitoring compositional or structural changes of the forest over time or for impact assessment. This information, along with the "Checklist of the Plant of Kaieteur National Park, Guyana" provides data on the plant taxa found on the Potaro Plateau in the vicinity of Kaieteur National Park. In addition to minimizing habitat damage due to industrial development, these data can be used to provide the framework for conservation efforts in the park as well as for the development of ecotourism.

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BOOK NOTICE

Rafaël Govaerts and David A. Simpson, with Jeremy Bruhl, Tatyana Egorova, Paul Goetghebeur, and Karen Wilson. 2007. **World Checklist of Cyperaceae: Sedges.** (ISBN 978-1-84246-199-0 pbk.). Royal Botanic Gardens, Kew, Richmond, Surrey, TW9 3AB, United Kingdom. (**Orders:** www.kewbooks.com, publishing@kew.org). $196.00, 765 pp., 9" × 6".

Contents:

- Introduction
- How to use the Checklist
  - Structure
  - Names
  - Acceptance of taxa
  - Geographical distribution
  - Life-forms
- Abbreviations
- Acknowledgments
- Co-authors
- References
- Cyperaceae
- Unplaced Names

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REDISCOVERY OF *MIRABILIS HINTONIORUM* (NYCTAGINACEAE), A STRIKING FOUR-O'CLOCK ENDEMIC TO THE SIERRA DE COALCOMÁN, MICHOACÁN, MEXICO

Mark Fishbein

Department of Biology and Herbarium
Portland State University
P.O. Box 751
Portland, Oregon 97207, U.S.A.
mfish@pdx.edu

Victor W. Steinmann

Instituto de Ecología
Centro Regional del Bajío
61600, Pátzcuaro, Michoacán, MEXICO

ABSTRACT

Recent collecting in the Sierra de Coalcomán, Michoacán, Mexico, resulted in the rediscovery of *Mirabilis hintoniorum*, a species that had not been recollected since its first gathering in 1939. The rediscovery is notable because of the striking flowers of the species, which are unusual in the genus by virtue of their nearly limbless, tubular form and "firecracker" red and yellow colors. The species is undoubtedly rare and likely endemic to the Sierra de Coalcomán.

RESUMEN

En una salida a la Sierra de Coalcomán, Michoacán, México resultó el redescubrimiento de *Mirablis hintoniorum*, una especie que no había sido encontrada desde la primera colecta hecha en 1939. El redescubrimiento es notable dado que es una especie muy atractiva por sus flores, las cuales son tubulares, con lóbulos reducidos y con una mezcla de amarillo y rojo. La especie es muy rara y endémica de la Sierra de Coalcomán.

From 1931 to 1941, famed plant collector George B. Hinton (1882–1943) conducted extensive botanical exploration, primarily in the southern Mexican states of Guerrero, México, and Michoacán. During this time he made over 16,000 collections, and his specimens have served as the types of more than 360 species (Hinton & Rzedowski 1975). On July 11, 1939 Hinton secured specimens in the Sierra de Coalcomán, in southwest Michoacán, of what is undoubtedly the most striking of all species of four-o'clocks (*Mirabilis* L.). Despite the distinctiveness and showiness of the species, and the several duplicate specimens that were distributed to major herbaria, the species remained "undiscovered" by taxonomists until Le Duc (1992) described *Mirabilis hintoniorum* Le Duc over 50 years later. In the course of monographic work on *Mirabilis* section *Mirabilis*, Le Duc came across four duplicates of Hinton's collection, housed in herbaria at the University of Texas (TEX), Conservatory and Botanical Garden of Geneva (G), Missouri Botanical Garden (MO), and University of California, Berkeley (UC). When she published her monograph in 1995, Le Duc had not encountered additional collections of *M. hintoniorum* (Le Duc 1995). In this note, we provide a fuller description and photographs of this remarkable species that had apparently not been recollected until we, too, encountered plants in the Sierra de Coalcomán.

Although unremarkable in vegetative morphology, *M. hintoniorum* is unrivaled among the nearly 60 species in the genus by virtue of the form and color of the flowers. Le Duc distinguished *M. hintoniorum* from similar species on the basis of glabrous, few-flowered inflorescences and the exceedingly shallow lobes and orange color of the perianth. However, her observations, based only upon examination of few herbarium specimens and Hinton's economical observations on the specimen labels, are not entirely accurate and fail to convey the spectacular impression of the living plants. In particular, the inflorescences are hardly few-flowered and the perianth scarcely orange.

On June 28, 2003 we collected *Mirabilis hintoniorum* for apparently the first time since Hinton encountered the species 64 years earlier. Had we been familiar with Hinton's collection or Le Duc's description of the species, we would have been wholly unprepared for the appearance of this seeming botanical fireworks display (Figs. 1–3). The flowers, described by Hinton as simply "orange", are in actuality pendent flames—

Fig. 1. ***Mirabilis hintoniorum*** **Le Duc photographed in the Sierra de Coalcomán, Michoacán, México. 1. habit.**

the perianth tube is bright red, grading into a vibrant yellow with red venation in the limb. However, these features are lost with drying, and the flowers on both Hinton's and our herbarium collections are nearly colorless. In contrast to the "few-flowered" inflorescences (Le Duc 1992, 1995) of Hinton's specimens, those on the plants that we encountered comprise a many-flowered, pyrotechnic cascade. To Le Duc's otherwise accurate description we can add that the plants are erect, bushy, perennial herbs reaching 1 m in height with red stems. In addition to the aforementioned characteristics of the flowers, the stigmas are pink and the anthers red.

Like Hinton, we encountered *M. hintoniorum* only in the Sierra de Coalcomán. Whereas the type locality of Villa Victoria is along the Pacific Slope, our initial encounter took place approximately 55 kilometers (airline) away, at the opposite (northeastern) end of the range within the Balsas Depression. We were brought to an abrupt stop by the sight of *M. hintoniorum* while traveling along the unpaved road from Aguililla at the foot of the mountains to the high-mountain logging town of Dos Aguas. As we approached the unknown marvel, we were dumbstruck with the realization that we were gazing at a *Mirabilis* dramatically unlike any that either of us had ever seen, the myriad cultivars of *M. jalapa* L. not excepted. Only a small patch of these robust plants was found at this site, which we documented with several specimens (*Fishbein and Steinmann 5113*). Later the same day, we observed another small patch on the southwestern side of the range, between Dos Aguas and Coalcomán along the road to Villa Victoria, from which no collections were made. We did not observe the species anywhere else.

It is paradoxical that *M. hintoniorum*, arguably the showiest species in the genus, should have remained so obscure, notwithstanding being a narrow endemic to the Sierra de Coalcomán. Two populations were

FIGS. 2–3. *Mirabilis hintoniorum* Le Duc photographed in the Sierra de Coalcomán, Michoacán, México. 2 (top). flowering stems. 3 (bottom). close up of flowers.

found along a moderately traveled, albeit rugged, road that has been traversed periodically by plant collectors, including Rogers McVaugh. In fact, we made our collection at the type locality of *Ipomoea fissifolia* (McPherson) Eckenw. It seems likely that the species is indeed endemic to the Sierra de Coalcomán and it is quite likely rare. Furthermore, it possibly has a very brief flowering span in the early part of the rainy season, and these factors may help to explain not only the few encounters by plant collectors but also the absence of the "firecracker four-o'clock" from our gardens.

Exsiccatae. **MÉXICO. Michoacán.** Distr. Coalcomán: Villa Victoria, alt. 700 m, dense woods, 11 Jul 1939, *G.B. Hinton et al. 13909* (holotype: TEX; isotypes: G, MO, photo!, UC); Mpio. Aguililla, along Aguililla-Dos Aguas road, 18.2 km (road) WSW of La Paz at jct Apatzingán-Aguililla road, 18°46.0'N 102°50.90'W, elev. 1500 m, roadcut, heavily disturbed upper tropical deciduous forest just below transition to oaks, with *Guazuma, Heliocarpus, Pouzolzia, Oxalis, Gonolobus grandiflorus, Opuntia, Cordia*, 28 Jun 2003, *M. Fishbein & V.W. Steinmann 5113* (ARIZ!, F!, HPSU!, IEB!, MEXU!, MISSA!, MO!).

ACKNOWLEDGMENTS

We used the Missouri Botanical Gardens' w^{3}TROPICOS database (mobot.mobot.org/W3T/Search/vast.html) to examine an image of MO's isotype of *Mirabilis hintoniorum*. We thank Ignacio García, Guy Nesom, and Richard Spellenberg for reviewing the manuscript and providing helpful suggestions. Fishbein's fieldwork was supported in part by the Department of Biological Sciences, Mississippi State University, and Steinmann's studies were supported by a grant from the Comisión Nacional para el Conocimiento y Uso de la Biodiversidad to the Instituto de Ecología (account number 20007).

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FLORISTIC COMPOSITION OF SEASONALLY DRY TROPICAL FOREST FRAGMENTS IN CENTRAL BAHIA, NORTHEASTERN BRAZIL

Domingos Benício Oliveira Silva Cardoso
Herbário da Universidade Estadual de Feira de Santana (HUEFS)
Km 03-BR 116, Campus. 44031-460
Feira de Santana, Bahia, BRAZIL
cardosobot@gmail.com.br

Luciano Paganucci de Queiroz
Universidade Estadual de Feira de Santana
Depto. de Ciências Biológicas, Herbário da Universidade Estadual de Feira de Santana (HUEFS)
Km 03-BR 116, Campus. 44031-460
Feira de Santana, Bahia, BRAZIL
lqueiroz@uefs.br

ABSTRACT

The Serra do Orobó Mountain range is located in central Bahia State, northeastern Brazil, and occupies an area of approximately 7,300 ha. The range comprises different physiognomies of Seasonally Dry Tropical Forest (SDTF), including semideciduous and riparian forests that grow on the lower slopes at elevations (450 to 700 meters) and fragments of submontane humid forest growing near the summit (700 to 850 meters). A floristic survey was undertaken at the 15 best preserved forest fragment sites scattered along the Orobó range. A total of 615 species within 378 genera and 106 families were sampled, including ten new angiosperm taxa. Angiosperms comprised 597 species within 365 genera and 96 families, while pteridophytes comprised 18 species in 13 genera and 10 families. The floristic diversity of the Orobó site was high in comparison to other SDTF areas in eastern Brazil. Analyses of endemism and floristic relationships suggested that the flora of the seasonally semideciduous forests of the Serra do Orobó mountain range is more closely related to the seasonally dry forest vegetation of the Atlantic Forest domain rather than to the Caatinga domain.

RESUMEN

La Serra do Orobó es un macizo montañoso localizado en el área central del estado de Bahia, región nororiental del Brasil, que ocupa una área de aproximadamente 7.300 ha. Comprende fisonomías diferentes del Bosque Tropical Estacionalmente Seco (SDTF), incluyendo principalmente los bosques semideciduos y los bosques riparianos que crecen en los declives inferiores en elevaciones entre 450 y 700 metros, y un fragmento de bosque submontano húmedo cerca de la cúspide entre 700 y 850 metros. Fue llevado a cabo un estudio florístico en 15 sitios que presentaban fragmentos en buen estado de conservación a lo largo de la Serra do Orobó. Fueron muestreados un total de 615 especies en 378 genera y 106 familias, incluyendo diez nuevos taxa de diferentes familias de angiospermas. Las angiospermas abarcan 597 especies en 365 genera y 96 familias y las pteridofitas incluyeron 18 especies en 13 genera y 10 familias. La diversidad floristica fue alta comparado con otras áreas de SDTF en el Brasil Oriental. Los análisis de endemismo y de relaciones floristicas sugieren que la flora del bosque estacionalmente semideciduo de la Serra do Orobó se relaciona más a la vegetación del bosque seco del dominio de la Floresta Atlántica que al del dominio de las Caatingas.

INTRODUCTION

Seasonally Dry Tropical Forests (SDTF) are one of the world's most threatened ecosystems. Miles et al. (2006) observed that ca. 97% of these dry forest remnants are at risk for biodiversity loss due to a number of different anthropogenic threats, such as habitat fragmentation, climatic change, fire, or conversion into cultivated areas. However, SDTF have received relatively little attention from conservationists and ecologists in comparison to humid forests (Pennington et al. 2006b).

Little is presently known about the floristic diversity of neotropical SDTF although in recent years there has been an increasing interest in this vegetation type (Gentry 1995; Giulietti et al. 2006; Pennington et al. 2006a). However, the growing knowledge of the SDTF flora has stimulated the formulation of various hypotheses concerning the historical biogeography of this vegetation (Prado & Gibbs 1993; Pennington et al. 2000, 2004; Prado 2000; Lavin et al. 2004; Queiroz 2006a) and the geographical distribution of its component species, and studies have indicated that SDTF are independent phytogeographical units distributed disjunctly through South and Central America (Pennington et al. 2000; Prado 2000).

According to the definition elaborated by Pennington et al. (2000), the neotropical SDTF comprehend different physiognomies, and can include both forests as well as more open vegetation types where shrubs predominate. Terrestrial bromeliads and succulent plants belonging to Cactaceae and Euphorbiaceae are

common in SDTF areas, as well as an ephemeral herbaceous component apparent only during the short rainy season. Another important aspect characterizing SDTF is their markedly seasonal phenology of flowering and fruiting, with many species demonstrating synchronous flowering at the transition between the dry and the rainy seasons (Machado et al. 1997).

The Caatinga domain constitutes the largest and most isolated nucleus of the SDTF (Queiroz 2006a). It occupies ca. 800,000 Km^2 in the northeastern section of Brazil (Ab'Sáber 1974) with a semi-arid climate mainly in the low altitude areas between extensive plateaus and/or mountain ranges (Prado 2003; Queiroz 2006a). Andrade-Lima (1981) noted that the vegetation of the Caatinga domain comprised different physiognomies, including areas of open vegetation dominated by shrubs or areas with relatively tall forests. These seasonally dry forests are commonly referred to as arboreal caatinga, dry forests, or deciduous forests, and occur as highly fragmented areas throughout the semi-arid region of northeastern Brazil, principally from Bahia State through northern Minas Gerais State. In spite of the fact that these dry tall forest areas are situated within the Caatinga domain (Rizzini 1979; Andrade-Lima 1981), different workers have indicated that they may in fact be phytogeographically more related to the dry vegetation of the Atlantic Forest domain (Oliveira-Filho & Fontes 2000; Amorim et al. 2005; Oliveira-Filho et al. 2005, 2006), or may represent disjunct areas of SDTF without any relationship to the humid areas of the Atlantic Coastal Forests (Pennington et al. 2000; Prado 2000). The deciduous and semi-deciduous forests of southern and southeastern Brazil, for example, have been demonstrated to have a strong floristic relationship with the moister sites of Atlantic Coastal Forest and therefore should not be treated as a type of dry tall forest included in the Caatinga domain (Oliveira-Filho & Fontes 2000; Oliveira-Filho et al. 2005). However, Oliveira-Filho et al. (2006) have more recently proposed a wider definition for SDTF that would treat these same deciduous and semi-deciduous forests of the Atlantic Forest domain as another nuclei of SDTF.

As such, it is clear that there are still problems to be resolved concerning the nature of SDTF in eastern South America. The delimitation of SDTF is complicated by the fact that Penington et al. (2000) and Prado (2000) did not include humid forests in their analyses, while Oliveira-Filho et al. (2006), on the other hand, included only a very limited sampling of Caatinga areas. Additionally, the knowledge concerning the floristic composition of many areas of SDTF in northeastern Brazil is still very incipient.

As such, the present study undertook a floristic survey of several fragments of seasonal dry forests in the Serra do Orobó Mountains in central Bahia State. The floristic relationships of these dry forests will be discussed here in terms of the present understanding of the phytogeography of SDTF. Specifically, we intend to demonstrate that the dry forest framents of the Serra do Orobó Mountains are floristically related to the SDTF floras. To account this goal, we will treat the SDTF as a broader definition (sensu Oliveira-Filho et al. 2006) that encompasses the dry sites of the Atlantic Forest domain as a distinct nuclei from the Caatinga domain and discuss the relationships of the Serra do Orobó mountain range with these former nuclei.

Study Area

The Serra do Orobó mountain range is located within the municipalities of Ruy Barbosa and Itaberaba in central Bahia State, Brazil (12°15' – 12°25'S and 40°19' – 40°30'W) (Fig. 1). The range occupies an area of approximately 7,300 ha and has a maximum elevation of 1,014 m (BAHIA 2002). The region has a semi-arid climate (SEI 1998), and although there are no systematic rainfall records for this area, estimates of precipitation in the region place the average annual rainfall at approximately 800 mm (SEI 1998). The average annual temperature is 26 °C, with an absolute maximum of 33 °C, and an absolute minimum of 18 °C (SEI 1998). The forest fragments examined have shallow soils that are sometimes covered by a significant layer of leaf litter. These soils are classified in the main group "luvisoil" and present moderate to high pH and nutrient levels (IBGE/EMBRAPA 2001). In addition, they are comparatively more fertile than those of the nearby savannas.

The Serra do Orobó mountain range is located within the Caatinga domain of northeastern Brazil (Velloso et al. 2002), and several vegetation types can be found there (Fig. 2) according to general altitudinal gradients. A shrubby caatinga with palm trees is most common at lower altitudes, while forests occur

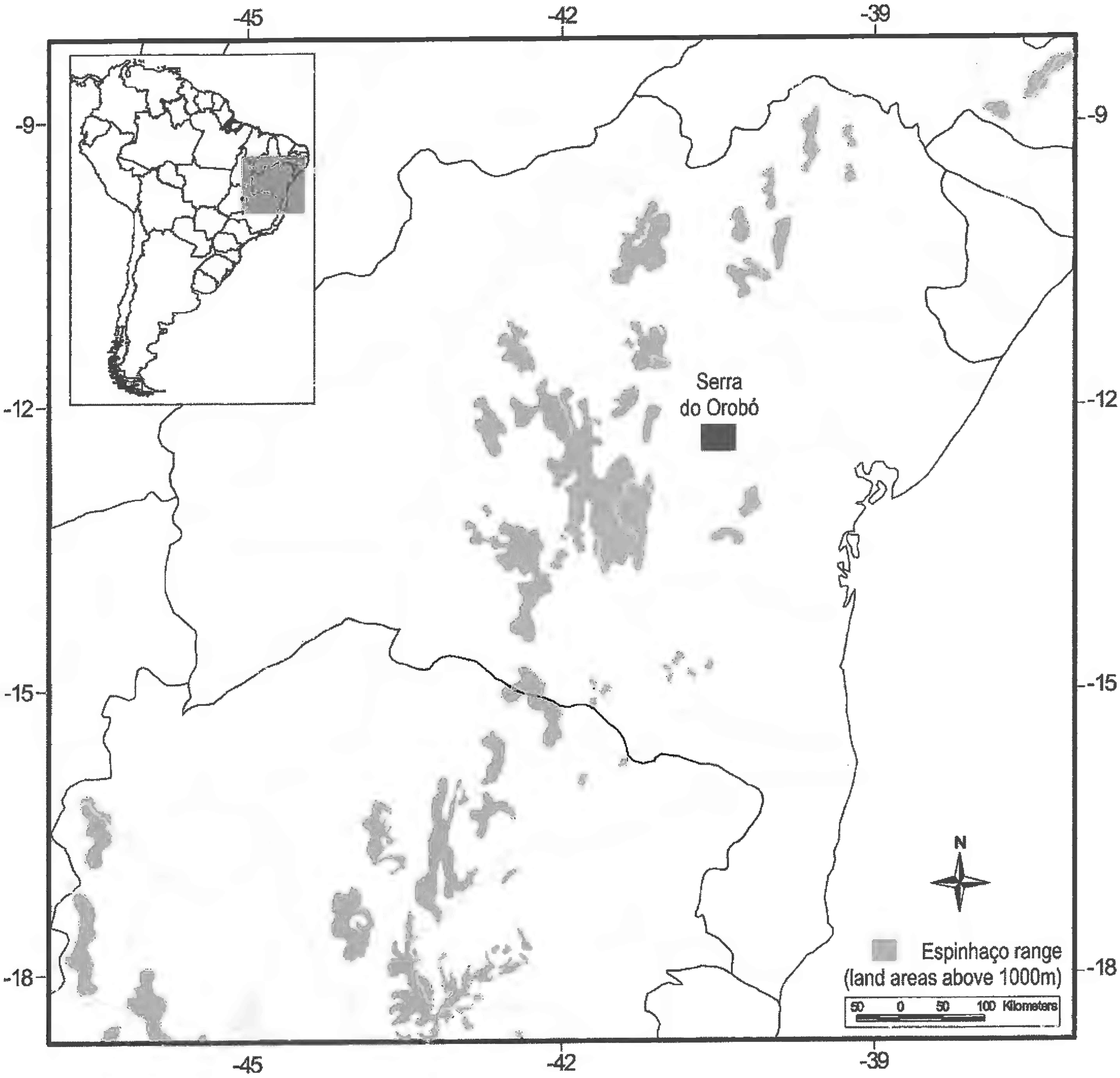

Fig. 1. The localization of the Serra do Orobó Mountains, near the Chapada Diamantina, central Bahia State, Brazil.

at higher altitudes (between 450 and 850 meters). Dry forest fragments and riparian forests are found on the slopes at elevations between 450 and 700 meters. There is a more humid area near the summit on the southern slope (between 700 and 850 meters) harboring a submontane humid forest. Above the forest zone, and surrounding the mountain peaks up to the 900 meters, is a savanna-like vegetation with large populations of *Vellozia furcata* L.B.Sm. & Ayensu (Velloziaceae). Near the summit, the rock outcrops harbor *campo rupestre* (rocky field) vegetation.

Although the Serra do Orobó has suffered strong anthropogenic alterations in 400 years of European colonization, some forest fragments are still relatively well-preserved. These fragments have extremely high conservation value as they represent some of the last intact fragments of dry forest in northeastern Brazil. Additionally, many new species belonging to different groups, such as the fungi (*Neojhonstonia minima*, Gusmão & Grandi 2001), psychodid flies (*Psychoda serraorobonensis*, Bravo et al. 2006) have been described from this area. Besides, some new species of plants from the *campo rupestre* vegetation were identified and are in process of publication (*Calliandra*, Fabaceae–E.R.Souza & L.P.de Queiroz, pers. comm.; two new

Fig. 2. Different forest physiognomies found in the Serra do Orobó Mountains, Bahia State, Brazil. A. A fragment of semideciduous forest; B. Riparian forest extending almost to the top of the mountain, with *Eriotheca* cf. *globosa* in bloom; C. A fragment of humid forest covered by fog; D. Interior of the humid forest, showing many epiphytes.

species of *Marcetia*, Melastomataceae–A.K.A.Santos, pers. comm.; *Mitracarpus*, Rubiaceae–E.B.Souza, pers. comm.; *Oncidium*, Orchidaceae–C.van den Berg, pers. comm.; and *Sauvagesia*, Ochnaceae–D.Cardoso, pers. comm.).

In 2002, the forest remnants as well as the *campo rupestre* vegetation of the Serra do Orobó mountain range were assigned the status of sustainable use protection areas in recognition of their importance to conservation and to biodiversity research.

METHODS

A floristic survey was carried out from August 2004 to June 2006 in the best preserved sites of semideciduous, riparian, and submontane humid forest fragments. The vegetation classification used here for each forest fragment follows Veloso et al. (1991) and stresses the distinct physiognomies and ecological conditions observed in each. It was studied 8 fragments of semideciduous forests (2.85 km^2), 6 of riparian forests (0.37 km^2) and one of submontane humid forest (0.07 km^2).

During the course of the present study a total of 15 field trips were carried out, each lasting from three to four days. Of all the 15 studied fragments, the submontane humid forest one was the unique where our collect effort was lower due to its difficult access and because it was discovered only recently. All fertile material of vascular plants was collected according to the standard methods described by Filgueiras et al.

(1994). In some cases, sterile collections were made for species never encountered with flowers or fruits. A total of 1,385 voucher collections were made and subsequently stored at the Feira de Santana State University Herbarium (HUEFS). In some cases, species that were very difficult to collect were included in the checklist if they could be positively identified in the field; these are indicated as "Not collected" in Appendix 1.

All specimens were identified by the authors with the aid of identified collections stored at the HUEFS and/or by using specific bibliographies. Specimens identified only to genus or family, are clearly labeled in the Appendix. Duplicates were sent to specialists in order to provide or to confirm identifications.

Angiosperm families are organized according to APG II (2003) in the floristic list, and the pteridophytes according to Tryon and Tryon (1982). Authors of species are abbreviated according to Brummit and Powell (1992).

RESULTS

The vascular flora of the forest vegetation of the Serra do Orobó mountain range comprises 615 species belonging to 378 genera and 106 families (Appendix 1). Angiosperms are represented by 597 species in 365 genera and 96 families. The pteridophytes included 18 species belonging to 13 genera and 10 families. A total of 561 taxa were identified to species rank (91.2%). However, in some groups (especially the Myrtaceae), many taxa were identified only to the genera (51 specimens, or 8.3% of the total collection) or family rank (3 specimens, 0.5%) due to their taxonomic difficulty.

The semideciduous forests demonstrated the greatest species richness (465 spp.), while 141 and 87 species were sampled in the riparian and in the submontane humid forests, respectively. Considering all forest fragments together, the commonest life form was trees (182 species), followed by vines (138), herbs (111), shrubs (104), subshrubs (45), and epiphytes (35). The most diverse families were Fabaceae (95 species), Euphorbiaceae (38), Apocynaceae (24), Orchidaceae (24), Rubiaceae (24), Asteraceae (22), Bignoniaceae (19), Myrtaceae (18), Malvaceae (17), and Rutaceae (15), which together comprised 48% of the total number of species surveyed in the Serra do Orobó mountain range. Thirty-five families were represented by only a single species. The most species-rich genera were *Croton* (11 species), *Passiflora* (8), *Senna* (8), *Eugenia* (7), *Myrcia* (7), *Solanum* (7), *Miconia* (6), *Bauhinia* (5), and *Senegalia* (5).

Several species were identified by different specialists as being new taxa (Fig. 3). These included: *Dorstenia caatingae* (Moraceae; Castro & Rapini 2006), *Phanera trichosepala* (Fabaceae, Queiroz 2006b), and undescribed species belonging to the genera *Cratylia* (Fabaceae–L.P.de Queiroz, pers. comm.), *Conchocarpus* (Rutaceae–J.R.Pirani, pers. comm.), *Dichorisandra* (Commelinaceae–L.Aona, pers. comm.), *Eugenia* (Myrtaceae–M.Sobral, pers. comm.), *Sinningia* (Gesneriaceae–A.Chautems, pers. comm.), *Solanum* (Solanaceae–L.P.de Queiroz & D.Cardoso, pers. comm..), *Standleya* (Rubiaceae–J.G.Jardim, pers. comm.), and *Spermacoce* (Rubiaceae–E.B.Souza and E.L.Cabral, pers. comm.). Additionally, of the total number of species collected, 12 were considered to be endemic to the dry forest fragments of Serra do Orobó or to the adjacent dry forest areas. These species are marked by an asterisk in the Appendix 1.

In addition to these new species, other taxa were collected for the first time in Bahia State, including *Bulbophyllum sanderianum* (Orchidaceae), *Croton warmingii* (Euphorbiaceae), and *Oxalis roselata* (Oxalidaceae) (Fig. 3). Other interesting collections included *Cordia blanchetii* (Boraginaceae), *Heteranthia decipiens* (Solanaceae), and *Passiflora bahiensis* (Passifloraceae), which were only previously known from their type material collected in Bahia; as well as *Pogoniopsis schenckii* and *Wullschlaegelia calcarata*, both very uncommon saprophytic orchids (Fig. 3).

The forest fragments were composed of different plant strata. In general there was a continuous canopy ca. 20 meters high, composed of *Aspidosperma parvifolium* (Apocynaceae), *Cariniana estrellensis* (Lecythidaceae), *Centrolobium tomentosum* (Fabaceae), *Cnidoscolus oligandrus* (Euphorbiaceae), *Ficus pulchella* (Moraceae), *Heisteria blanchetiana* (Olacaceae), *Hirtella glandulosa* (Chrysobalanaceae), *Nectandra* cf. *membranacea* (Lauraceae), *Myrsine ferruginea* (Myrsinaceae), *Peltogyne confertiflora* (Fabaceae), *Piptadenia paniculata* (Fabaceae), and *Vantanea compacta* (Humiriaceae). Emergent trees could reach up to 30–45 meters, and included *Eriotheca*

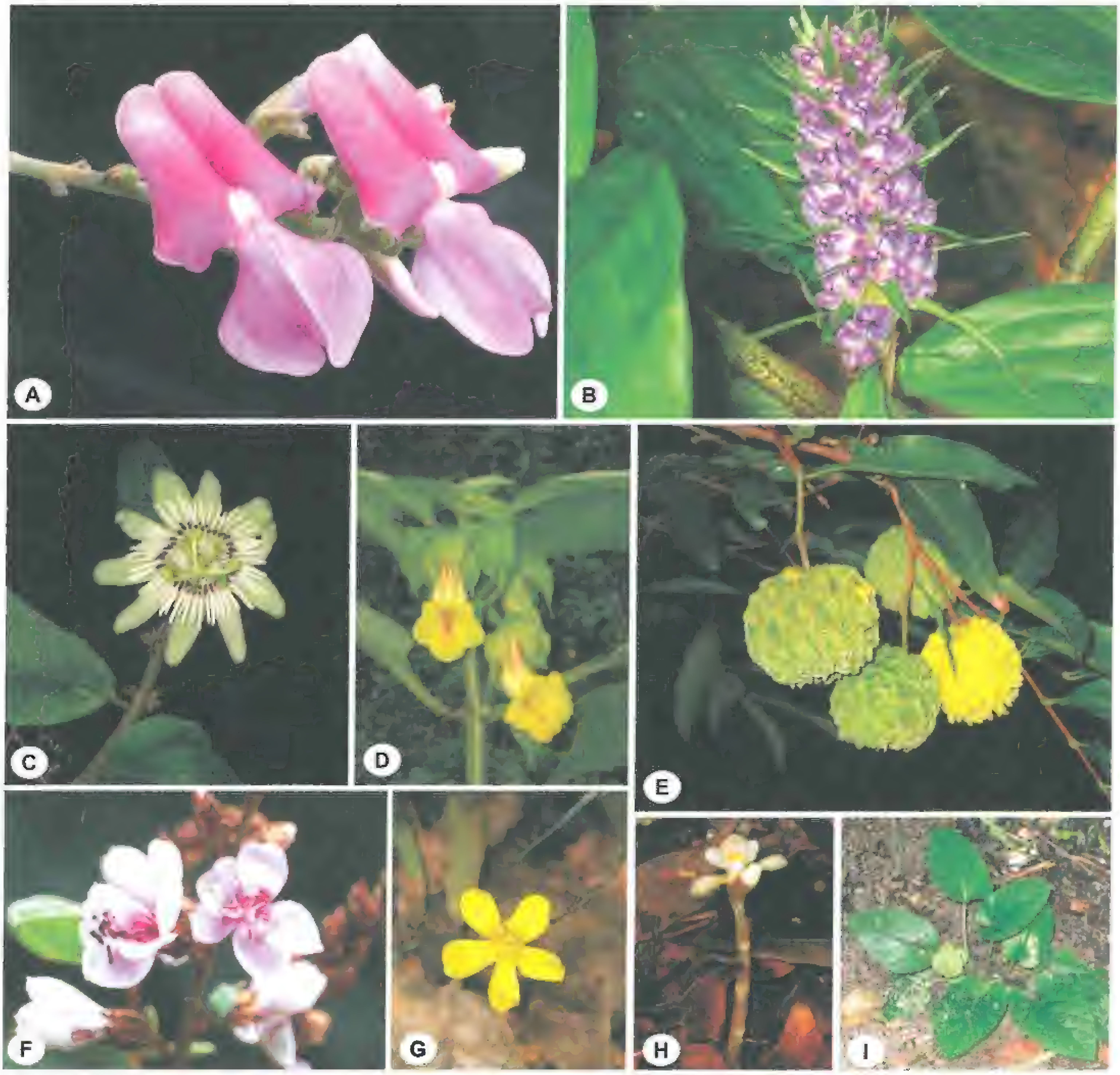

Fig. 3. Some representatives of the flora of the Serra do Orobó Mountains. A. ***Cratylia*** **sp. nov.; B.** ***Dichorisandra*** **sp. nov.; C.** ***Passiflora bahiensis*****; D.** ***Sinningia*** **sp. nov.; E.** ***Eugenia*** **sp. nov.; F.** ***Phanera trichosepala*****; G.** ***Oxalis roselata*****; H.** ***Pogoniopsis schenkii*****; I.** ***Dorstenia caatingae*****.**

cf. *globosa* (Malvaceae), *Caesalpinia leiostachya* (Fabaceae), *Cavanillesia arborea* (Malvaceae), *Ficus cyclophylla*, *F. gomelleira* (Moraceae), *Goniorrhachis marginata* (Fabaceae), *Vochysia* sp. (Vochysiaceae), and *Manilkara rufula* (Sapotaceae). Several vine species, mostly belonging to the families Apocynaceae, Bignoniaceae, Fabaceae, Passifloraceae, and Sapindaceae, occur in the canopy, within treefall gaps, or along the edges of the forest fragments. The subcanopy was dominated by species of Euphorbiaceae, Fabaceae, Myrtaceae, Melastomataceae, Rubiaceae, and Rutaceae.

The submontane humid forest fragment was the richest area for epiphytes, including *Anthurium pentaphyllum*, *A. scandens* (Araceae), *Nematanthus albus* (Gesneriaceae), *Oncidium ciliatum*, *O. flexuosum* (Orchidaceae), *Peperomia* sp. (Piperaceae), *Tillandsia stricta* (Bromeliaceae), and *Vriesea simplex* (Bromeliaceae). This submontane humid forest fragment also had a dense herbaceous stratum composed of sciophilous herbs such as *Paepalanthus spatulathus* (Eriocaulaceae), *Sinningia barbata* (Gesneriaceae), *Begonia petasitifolia* (Begoniaceae), *Dichaea congniauxiana* (Orchidaceae), *Sobralia sessilis* (Orchidaceae), *Gibasis geniculata* (Commelinaceae), *Ichnanthus grandifolius* (Poaceae), and *Ruellia affinis* (Acanthaceae).

The commonest species found at forest edges and in disturbed sites were the trees *Albizia polycephala* (Fabaceae) and *Maclura tinctoria* (Moraceae), the shrubs *Diospyros inconstans* (Ebenaceae), *Lantana camara* (Verbenaceae), and *Senna aversiflora* (Fabaceae), the vines *Arrabidaea cinerea* (Bignoniaceae), *Chaetocalyx scandens* (Fabaceae), *Dicella bracteosa* (Malpighiaceae), *Macroptilium erythroloma* Fabaceae), and *Periandra coccinea* (Fabaceae), and the herbs *Chaptalia integerrima*, *Emilia fosbergii* (Asteraceae), *Pavonia martii* (Malvaceae), *Hyptis pectinata*, and *H. suaveolens* (Lamiaceae).

Some tree species present in the best preserved forest fragments, such as *Gallesia integrifolia* ("pau-d'alho", Phytolaccaceae) and *Caesalpinia leiostachya* ("pau-ferro"), are used locally as folk medicines. Additionally, we found evidence of fully grown trees being harvested for their wood, including *Copaifera langsdorffii* ("pau-d'óleo", Fabaceae), *Brosimum guianense* ("oiticica", Moraceae), *Ocotea glomerata* ("lôro", Lauraceae), and *Hymenaea courbaril.* ("jatobá," Fabaceae).

DISCUSSION

Floristic diversity

The forest fragments of Serra do Orobó mountain range demonstrated a relatively higher number of species in comparison to other Brazilian semideciduous forests, even comparing the arboreal component only (Meira-Neto et al. 1989; Oliveira-Filho & Machado 1993; Soares-Filho 2000; Werneck et al. 2000; Jarenkow & Waechter 2001; Moura & Sampaio 2001; Cielo-Filho & Santin 2002; Paula et al. 2002; Silva & Soares 2002; Nunes et al. 2003; Souza et al. 2003; Andrade & Rodal 2004; Toniato & Oliveira-Filho 2004; Rodal & Nascimento 2006; Macedo 2007), or shrubby *caatinga* (Rodal et al 1998; Lemos & Rodal 2002; Pereira et al. 2002; Alcoforado-Filho et al. 2003; Nascimento et al. 2003; Andrade et al. 2004; Rocha et al. 2004), riparian forests (Vilela et al. 1995; Funch 1997; Passos-Júnior 1999; Stradmann 2000; Ribeiro-Filho 2002; Lacerda et al. 2005), or enclaves of humid forests within the *caatinga* (locally known as "brejo de altitude") (Tavares et al. 2000; Rodal & Nascimento 2002; Melo & Rodal 2003; Agra et al. 2004; Barbosa et al. 2004).

The species richness encountered in the submontane humid forest (87 spp.) was surprisingly lower than would normally be expected in this forest physiognomy in comparison with other studies (Mori 1989; Lombardi & Gonçalves 2000; Tavares et al. 2000; Carvalho-Sobrinho & Queiroz 2005; Amorim et al. 2005; Neves 2005; Martini et al. 2007), and lower also that observed in the dry and riparian forest fragments of the same mountain range. This may be due to the reduced size of the fragment examined, and/or to the relatively low sampling effort in this area. As such, more field trips to the area may reveal the presence of other species not yet recorded.

With minor variations, the ten most species-rich families in this survey were the same families identified as important in other SDTF sites, irrespective of the general aspects of the local climate, soil, and forest physiognomy. Similarly, several of these families (usually Fabaceae, Euphorbiaceae, Apocynaceae, Bignoniaceae, Myrtaceae, and Rubiaceae) were important in sand dune areas of the middle São Francisco river in northeastern Brazil (Nascimento et al. 2003; Rocha et al. 2004), in caatinga areas on sandy soils (Araújo et al. 1998; Rodal et al. 1998; Andrade et al. 2004), shrub caatinga areas on crystalline basement rocks (Pereira et al. 2002; Alcoforado-Filho et al. 2003), semideciduous forests in southeastern and southern Brazil (Jarenkow & Waechter 2001; Cielo-Filho & Santin 2002; Paula et al. 2002; Silva & Soares 2002; Toniato & Oliveira-Filho 2004), riparian forests in the Chapada Diamantina of Bahia State (Funch 1997; Passos-Júnior 1999; Stradmann 2000; Ribeiro-Filho 2002), as well as in several neotropical SDTF (Pennington et al. 2000; Bridgewater et al. 2003; Linares-Palomino et al. 2003). Fabaceae was the most species-rich family in the Serra do Orobó mountain range as well as in the other sites referred to above. Schrire et al. (2005) presented historical and biogeographical evidence supporting the hypothesis of a long term association between legumes and dry forests. Amongst the vines, the families with the greatest numbers of species in the Serra do Orobó (Apocynaceae, Bignoniaceae, Malpighiaceae, Fabaceae, and Sapindaceae) were also encountered in other semideciduous forest fragments (Hora & Soares 2002; Udulutsch et al. 2004). These too similar species richness at the family level encountered throughtout different physiognomies of dry vegetation in

Brazil as well as in the Central and northern South America may also be concerned for justifying that the Serra do Orobó mountain range should be included into a broad definition of SDTF.

On the other hand, a more restrict evaluation comparing the most species-rich genera may be suggestive to stress that within the different physiognomies of SDTF in eastern Brazil, the dry forest fragments of the Serra do Orobó Mountains should be floristically related to the semideciduous forests of the Atlantic Forest domain rather than to the dry shrub-arboreal vegetation of the Caatinga domain. For example, most of the genera comprising the largest numbers of species identified in this survey, such as *Croton*, *Passiflora*, *Miconia*, *Myrcia*, *Eugenia*, *Solanum*, and *Bauhinia* are better represented in several areas of semideciduous forests (e.g. Soares-Filho 2000; Paula et al. 2002; Silva & Soares 2002; Nunes et al. 2003; Andrade & Rodal 2004; Amorim et al. 2005; Macedo 2007) than in shrub-arboreal caatinga areas (Araújo et al. 1998; Rodal et al. 1998; Lemos & Rodal 2002; Pereira et al. 2002; Alcoforado-Filho et al. 2003; Cardoso & Queiroz, unpublished data). Moreover, the paucity of Cactaceae species in the Serra do Orobó Mountains is another evidence for lack of closer relationship with the Caatinga domain, where this family is usually abundant (see for example Taylor & Zappi 2002; Rocha et al. 2004; Gomes et al. 2006).

Endemism

Among the 152 arboreal species surveyed in the dry forest fragments in the Serra do Orobó Mountains, 16 (see Appendix 1) are conspicuous representatives of the SDTF flora (Prado & Gibbs 1993). Besides, the genera *Apuleia* (Fabaceae), *Brasiliopuntia* (Cactaceae), and *Pterogyne* (Leguminosae) surveyed here are endemic to the SDTF as a whole (Prado 2000). In addition, another 14 species considered endemic to the caatinga domain occur in the dry forest fragments of the Serra do Orobó Mountains or in other nearby areas, such as *Anemopaegma laeve* (Bignoniaceae), *Apodanthera glaziovii* (Cucurbitaceae), *Averrhoidium gardnerianum* (Sapindaceae), *Capparis jacobinae* (Brassicaceae), *Heteranthia decipiens* (Solanaceae), and *Senna acuruensis* var. *caatingae* (Fabaceae) (Giulietti et al. 2002). This highlights that the Serra do Orobó Mountains may be indeed related to the other remmants of seasonlly dry forests of the neotropics.

The presence of a considerable number of new species (ten) in the dry forest fragments in the Serra do Orobó Mountains may be explained in term of the processes of metacommunities, a model recently put forward for explaining the maintenance of diversity within SDTF (Lavin et al. 2004; Schrire et al. 2005). These authors propose that the biogeography of the succulent biome (which includes neotropical SDTF) can be better understood on a global scale by postulating metacommunities than by proposing historical processes of speciation due to climatic changes or tectonic movements. According to this model, SDTF occur in isolated areas (i.e. much like islands isolated within the continental area), with each area functioning like a local community that is linked to other areas through species exchange based on random dispersal events. The more extreme environmental conditions in SDTF restrict colonization by species originating in most other vegetation formations (Lavin et al. 2004), limiting the rate of immigration into a given local community and resulting in floras that are locally endemic. These processes also result in genera with very few species in local SDTF communities, in contrast with those observed in humid forests (Lavin 2006). For example, the most diverse genera in SDTF (e.g. *Senegalia*, *Croton*, *Machaerium*, *Mimosa*, *Senna*, and *Zanthoxylum*) usually do not comprise more than ten species in any given forest area (see Werneck et al. 2000; Nascimento et al. 2003; Rodal & Nascimento 2002; Bridgewater et al. 2003; Linares-Palomino et al. 2003; Melo & Rodal 2003; Rodrigues et al. 2003; Santos & Kinoshita 2003; Andrade & Rodal 2004; Lemos 2004; Rocha et al. 2004; and this study), while the most diverse genera in humid forests (e.g. *Eugenia*, *Inga*, *Miconia*, *Myrcia*, *Pouteria*, *Psychotria*, and *Solanum*) can have from 15 to even 27 species of the same genus occurring in the same locality (see Amorim et al. 2005; Neves 2005; Moreno et al. 2003; Lombardi & Gonçalves 2000; Oliveira & Amaral 2004; Martini et al. 2007).

The dry forests of Brazil are distributed in a fragmented and isolated fashion (very much like islands), which has led to the appearance of a significant number of endemic species. For example, 12 species encountered in this study had distributions limited to the forest fragments of the Serra do Orobó Mountains and adjacent areas. As such, we suggest that the endemism observed in these forests can be explained (on

a regional level) by the processes of metacommunities, in much the same way as species exchange has been proposed on a continent scale (Lavin et al. 2004; Lavin 2006; Schrire et al. 2005). In that context, the forest vegetation of the Serra do Orobó Mountains as a whole could be viewed as a local community that is isolated from other dry forest fragments found in eastern Brazil. Additionally, the recognition that this set of dry forest fragments (together with the Serra do Orobó Mountains) is a regional metacommunity is supported by the presence of disjunct species among the different areas—a pattern that has been similarly observed at a continental scale among the different nuclei of SDTF (Pennington et al. 2006b; Lavin et al. 2004). *Cordia blanchetii*, for example, has only been observed in the Serra do Orobó Mountains and in another dry forest fragment in Jequié, Bahia State; *Passiflora bahiensis* has been recorded only in a few collections from an urban forest fragment in Salvador, Bahia; *Croton warmingii* demonstrates a disjunct distribution within other semi-deciduous forest fragments in southeastern Brazil; *Dimorphandra jorgei* and *Senna acutisepala* (Fabaceae) are known in Bahia only from a few semideciduous forest fragments in the southern part of that state; and *Margaritopsis carrascoana* (Rubiaceae) occurs in isolated areas of dry vegetation from Ceará State to northeastern Bahia.

Floristic relationships

Riparian forests.—These forests are closely associated with rivers and are widely distributed throughout Brazil, principally in the central region of the country (Oliveira-Filho & Ratter 1995), although local abiotic conditions may not always be adequate for the establishment of typical riparian forests (Rodrigues 2000). The riverside forests of the Serra do Orobó Mountains grow in steep and relatively narrow valleys. As such, their contact with the neighboring semideciduous forests is very great, and frequently results in intercalation with species commonly found in those forests, such as *Cupania rigida* (Sapindaceae), *Dictyoloma vandellianum* (Rutaceae), *Machaerium acutifolium* (Fabaceae), *Pera glabrata* (Euphorbiaceae), *Piper arboreum* (Piperaceae), *Shoepfia brasiliensis* (Olacaceae), and *Vitex* aff. *klugii* (Lamiaceae). However, a majority of the arboreal species encountered in the riparian forests occur only in this vegetation type. Many of the species occurring in the Serra do Orobó Mountains have been reported from riparian forests in the Chapada Diamantina in central Bahia (Funch 1997; Passos-Júnior 1999; Stradmann 2000; Ribeiro-Filho 2002) as, for example, *Bowdichia virgilioides* (Fabaceae), *Byrsonima sericea* (Malpighiaceae), *Clusia nemorosa* (Clusiaceae), *Ficus pulchella* (Moraceae), *Inga thibaudiana* (Fabaceae), *Pouteria ramiflora* (Sapotaceae), *Sloanea guianensis* (Elaeocarpaceae), *Simarouba amara* (Simaroubaceae), *Richeria grandis* (Euphorbiaceae), *Roupala montana* (Proteaceae), and *Vantanea compacta*. However, some species observed in the riparian forests of the Serra do Orobó Mountains are widely distributed within the riparian forests of central Brazil, such as *Copaifera langsdorffii*, *Hirtella glandulosa*, *Tapirira guianensis*, and the tree-fern *Cyathea delgadii* (Cyatheaceae) as noted by Oliveira-Filho & Ratter (1995). These same authors postulated that these riparian forests could act as ecological corridors linking the two principal nuclei of humid forests in South America (the Atlantic Coastal Forest and the Amazon Forest) due to their dendritic distribution throughout all of the Cerrado Biome in central Brazil.

Semideciduous and humid forest fragments.—The classification of the seasonal dry forests of northeastern Brazil is still a controversial subject. Andrade-Lima (1981) considered these forests as being related to arboreal caatinga, and thus part of the Caatinga domain. Prado (2000) and Pennington et al. (2000), based principally on the patterns of distribution of the arboreal species, adopted a similar circumscription, but considered the caatinga and the seasonal dry forests of eastern Brazil as part of a greater phytogeographical unit of the neotropics—the so common referred seasonally dry tropical forests (SDTF)—as distinct from the Atlantic Coastal Forest. This phytogeographical unit would comprise a large variety of vegetation formations, from tall forests in more humid areas to cactus scrub in the driest regions. This controversy can be clearly seen in the great variety of names applied to these different physiognomies, such as: tropical and subtropical dry forests, caatinga, mesotrophic, mesophilous or mesophytic forest, semideciduous or deciduous forest, *bosque caducifólio*, and thorn woodland (Pennington et al. 2000).

On the other hand, Oliveira-Filho et al. (2006) performed similarity analyses with areas of seasonal dry forests, shrub-arboreal caatinga, and humid Atlantic Coastal Forest areas, and identified greater floristic

affinity between seasonal dry forests and Atlantic Coastal Forest areas than with shrub-arboreal caatinga vegetation. As such, Oliveira-Filho et al. (2006) proposed a wider definition of SDTF of eastern South America that would include the three major floristic nuclei of dry vegetation formations: the Caatinga, the Chaco, and the seasonal forests of the Atlantic Forest domain, sensu latissimo.

An analysis of arboreal and shrub species distributions from semideciduous and humid forest fragments in the Serra do Orobó Mountains demonstrated that 106 species (46.5%) also occur in areas of the Atlantic Forest domain (sensu Oliveira-Filho et al. 2006), including *Chrysophyllum gonocarpum* (Sapotaceae), *Esenbeckia leiocarpa* (Rutaceae), *Lonchocarpus cultratus* (Fabaceae), *Myrcia rostrata* (Myrtaceae), *Swartzia apetala* (Fabaceae), and *Trichilia hirta* (Meliaceae). A total of 56 species (24%) were common to areas sampled in the Caatinga domain, and included *Aspidosperma pyrifolium* (Apocynaceae), *Mimosa tenuiflora*, *Poeppigia procera*, *Senna spectabilis* (Fabaceae), and *Ziziphus joazeiro* (Rhamnaceae) (Giulietti et al. 2006). Of these species, only nine of were considered as endemic to the Caatinga domain (Giulietti et al. 2002). Additionally, if considering all the 318 endemic species to the Caatinga domain cited by Giulietti et al. (2002), another eight non arboreal or shrub species occur in dry forest fragments of the Serra do Orobó Mountains or in other nearby areas. However, these 17 species make up only 4.5% of the total endemic flora of the Caatinga domain, suggesting that the dry forests of the Serra do Orobó Mountains might not be phytogeographically related to the Caatinga domain, but rather are of Atlantic Forest vegetation. Therefore, these numbers reinforce the hypothesis of Oliveira-Filho et al. (2006) that the semideciduous forests of eastern Brazil are floristically more closely related to the Atlantic Forest domain than to the Caatinga domain.

These suggestions are further strengthened by comparisons made between the flora of the Serra do Orobó Mountains and the Serra do Teimoso Reserve (a fragment of Atlantic Coastal Forest in southern Bahia State). The Serra do Teimoso Mountains, like the Serra do Orobó Mountains, have dry vegetation at their lower altitudes but more humid conditions exist at greater elevations, and the flora there is more closely related to the Atlantic Forest domain than to the SDTF sensu Pennington et al. (2000) (Amorim et al. 2005). Among the 252 arboreal species that occur in the Serra do Teimoso Mountains, 52 can also be found in the Serra do Orobó Mountains, including *Andira fraxinifolia* (Fabaceae), *Brasiliopuntia brasiliensis* (Cactaceae), *Brosimum guianense* (Moraceae), *Cavanillesia arborea* (Malvaceae), *Caesalpinia pluviosa, Centrolobium tomentosum*, *Goniorrhachis marginata* (Fabaceae), *Guapira opposita* (Nyctaginaceae), *Urera caracasana* (Urticaceae), and *Zanthoxylum rhoifolium* (Rutaceae). Examples of shrubs and herbaceous species held in common include: *Costus spiralis* (Costaceae), *Sinningia barbata* (Gesneriaceae), *Coccoloba declinata* (Polygonaceae), *Faramea hyacinthina* (Rubiaceae), and *Conchocarpus macrophyllus* (Rutaceae). Additionally, species such as *Croton warmingii* (Euphorbiaceae), *Dimorphandra jorgei* (Fabaceae), and *Heteropterys macrostachya* (Malpighiaceae) demonstrate a disjunct distribution pattern between the Serra do Orobó Mountains and the semideciduous forests within the Atlantic Forest domain.

Thus, while there exists significant data demonstrating a close phytogeographical relationship between the Serra do Orobó Mountains and the SDTF nuclei of seasonal dry forests within the Atlantic Forest domain, additional studies involving a larger number of areas also from the Caatinga domain would be useful in confirming some of the conclusions presented here.

APPENDIX 1

Species list of the plants found in semideciduous, riparian, and submontane humid forests of the Serra do Orobó Mountains, Bahia State, Brazil. The asterisk before the species names highlights the endemics from Serra do Orobó mountain range and/or adjacent dry forest areas and a circle refers to the representative arboreal species of SDTF according to Prado & Gibbs (2002). Abbreviations for vegetation types: SF: semideciduous, RF: riparian, and ShF: submontane humid forests; abbreviations for collectors are: LP=L.P.de Queiroz; C=D.Cardoso; N=F.R.Nonato; H=R.M.Harley; B=H.P.Bautista; P=G.C.P.Pinto; L=J.C.Lima; CO=T.A.B.Costa; RC=R.M.de Castro, and S=E.C.Smidt; abbreviations for life forms are: Sub=Subshrub; Epi=Epiphyte.

ANGIOSPERMS

Acanthaceae
Anisacanthus brasiliensis Lindau – LP 9383; Sub, SF
Justicia sp. – LP 9981; Herb, SF
Lepidagathis sp. – C 387; Sub, SF
Ruellia affinis Lindau – LP 10771; C 296; Vine, ShF
Ruellia bahiensis (Nees) Morong – C 381; Sub, SF

Agavaceae
Herreria salsaparilha Mart. – LP 12022; Vine, SF

Amaranthaceae
Alternanthera brasiliana (L.) Kuntze – LP 9538; Herb, RF
Gomphrena demissa Mart. – LP 9801; Herb, SF

Amaryllidaceae
Hippeastrum stylosum Herb. – C 835; Herb, SF

Anacardiaceae
Anacardium occidentale L. – LP 9392, 9434; Tree, SF
Spondias venulosa (Engl.) Engl. – LP 9470, 12028; Tree, SF
Tapirira guianensis Aubl. – LP 9778, 9802; C 343; Tree, RF, SF

Annonaceae
Oxandra reticulata Maas – LP 9788; Tree, SF
Rollinia emarginata Schltdl. – LP 9840; Tree, SF
Rollinia sylvatica (A.St.-Hil.) Mart. – LP 9967, 10663; C 1232; Tree, SF

Apocynaceae
Asclepias curassavica L. – LP 9551; Sub, SF
° *Aspidosperma discolor* A.DC. – C 1274, Tree, ShF
Aspidosperma parvifolium A.DC. – LP 9816, 12230; Tree, SF
° *Aspidosperma pyrifolium* Mart. – LP 9785; Tree, SF
Blepharodon nitidum (Vell.) J.F.Macbr. – LP 9876; C 356; Vine, RF, SF
Ditassa oxyphylla Turcz. – LP 9254, 10686; Vine, RF, SF
Forsteronia sp. – LP 10830; Vine, SF
Forsteronia glabrescens Müll.Arg. – C 1288; Vine, SF
Forsteronia pubescens A.DC. – LP 9944; Vine, SF
Gonolobus cordatus Malme – LP 10837; Vine, SF
Macroditassa adnata (E.Fourn.) Malme – LP 9264; Vine, RF
Mandevilla funiformis (Vell.) K.Schum. – C 270; Vine, SF
Mandevilla scabra (Hoffmanns. ex Roem. & Schult.) K.Schum. – C 324; Vine, RF
Matelea maritima (Jacq.) Woodson – LP 10643; Vine, SF
Oxypetalum erostre E.Fourn. – LP 10763; C 1289; Vine, SF
Oxypetalum pedicellatum subsp. *harleyi* Fontella & Goyder – LP 9851; C 767; Vine, SF
Peltastes peltatus (Vell.) Woodson – LP 12084; C 828; Vine, ShF, SF
Prestonia bahiensis Müll.Arg. – LP 9836; C 1293; Vine, SF
Prestonia coalita (Vell.) Woodson – LP 10689; C 378; Vine, SF
Rauvolfia bahiensis A.DC. – LP 10804, 12247; Tree, ShF
Schubertia multiflora Mart. – LP 10692; Vine, SF
Secondatia floribunda A.DC. – LP 9896; Vine, SF
Tabernaemontana solanifolia A.DC. – LP 9300, 9812; Tree, SF
Temnadenia violacea (Vell.) Miers – LP 9867; C 347; Vine, RF

Araceae
Anthurium pentaphyllum (Aubl.) G.Don – LP 12051; Epi, RF
Anthurium petrophilum K.Krause – C 272; Herb, SF
Anthurium scandens (Aubl.) Engl. – C 1275, Epi, ShF
Monstera adansonii var. *klotzschiana* (Schott) Madison – LP 12090, Epi, ShF
Philodendron pedatum (Hook.) Kunth – LP 9244, 9767; Epi, RF, SF

Arecaceae
Geonoma pauciflora Mart. – LP 9513; Shrub, RF
Geonoma pohliana Mart. – LP 12254; Shrub, ShF
Syagrus coronata (Mart.) Becc. – LP 9846; Tree, SF

Aristolochiaceae
Aristolochia eriantha Mart. & Zucc. – LP 9447; C 798; Vine, SF
Aristolochia gigantea Mart. & Zucc. – H 53484; LP 10668; C 376; Vine, SF

Asteraceae
Asteraceae sp. – LP 9940; Shrub, SF
Acanthospermum australe (Loefl.) Kuntze – C 792; Herb, SF
Achyrocline satureoides (Lam.) DC. – LP 10752; Sub, SF
Acritopappus confertus (Gardner) R.M.King & H.Rob. – LP 12249; Tree, ShF
Baccharis calvescens DC. – H 55454; Shrub, SF
Chaptalia integerrima (Vell.) Burkart – LP 9857; C 358; Herb, SF
Chromolaena cf. *laevigata* (Lam.) R.M.King & H.Rob. – LP 10678; Shrub, SF
Chromolaena morii R.M.King & H.Rob. – LP 10770; Shrub, SF
Cyrtocymura harleyi (H.Rob.) H.Rob. – H 55455; P 389; Shrub, SF
Cyrtocymura scorpioides (Lam.) H.Rob. – H 53480; LP 10709; Shrub, SF
Delilia biflora (L.) Kuntze – LP 10737; Herb, SF
Elephantopus sp. – LP 9543; Herb, RF
Emilia fosbergii Nicolson – C 1284; Herb, SF
Erechtites hieracifolia Raf. ex DC. – LP 12239, Sub, SF
Eremanthus capitatus (Spreng.) MacLeish – LP 12248; Tree, SF
Lepidaploa cotoneaster (Willd. ex Spreng.) H.Rob. – LP 9427; Sub, RF
Mikania cordifolia (L.f.) Willd. – LP 10816; Vine, ShF
Mikania elliptica DC. – LP 9508; Vine, RF
Mikania obovata DC. – C 1278; Vine, ShF
Verbesina macrophylla (Cass.) S.F.Blake – LP 9294; Sub, SF
Vernonanthura brasiliana (L.) H.Rob. – LP 9554; C 805; Shrub, RF, SF
Trixis antimenorrhoea (Schrank) Kuntze – LP 12278; Herb, SF

Begoniaceae
Begonia jairi Brade – LP 9403, 10787; Herb, ShF, SF
Begonia lobata Schott – LP 9925; C 247; Shrub, RF
Begonia petasitifolia Brade – LP 9768, 10751; Sub, RF, ShF
Begonia vitifolia Schott – LP 10790; Shrub, ShF

Bignoniaceae
Adenocalymma sp. – LP 12024; Vine, SF
Anemopaegma laeve DC. – LP 10832; Vine, SF
Arrabidaea craterophora (DC.) Bureau – LP 10677; Vine, SF
Arrabidaea cinerea Poepp. – LP 9253; C 278; Vine, RF, SF
Arrabidaea triplinervia (Mart. ex DC.) Baill. ex Bureau – C 1241; Vine, SF

Arrabidaea lasiantha Bureau & K. Schum. [= *Cuspidaria lasiantha* (Bureau & K. Schum.) A.H. Gentry comb. ined.] – C 280; Vine, SF
Cybistax antisyphilitica (Mart.) Mart. – LP 9475; Tree, SF
Fridericia speciosa Mart. – C 277; CO 17; Vine, SF
Handroanthus heptaphyllus (Vell.) Mattos – LP 12038; Tree, SF
Handroanthus ochraceus (Cham.) Mattos – LP 9969, 9998, 12016; Tree, SF
Jacaranda irwinii A.H.Gentry – C 318; Shrub, RF
Jacaranda jasminoides (Thunb.) Sandwith – LP 10724; Shrub, SF
Lundia cordata (Vell.) A.DC. – LP 10773; C 812; Vine, ShF, SF
Memora valida K.Schum. – LP 9784; B 1236; Vine, SF
Phryganocydia corymbosa (Vent.) Bureau ex K.Schum. – C 268, 276, 1282; Vine, SF
Piriadacus erubescens (DC.) Pichon – LP 9931; C 284; Vine, SF
Proterantha glandulosa A.H.Gentry [New undescribed genus] – LP 9799, 9901; Vine, SF
Tynanthus sp. – LP10681; C 357; Vine, SF
Tynanthus labiatus (Cham.) Miers – LP 10661; Vine, SF

Boraginaceae
* *Cordia blanchetii* DC. – LP 9448; C 770; Tree, SF
Cordia curassavica (Jacq.) Roem. & Schult. – H 53485; LP 9939; Shrub, SF
Cordia superba Cham. – LP 9932; C 383, 1254; Tree, SF
Heliotropium angiospermum Murray – LP 9979; Sub, SF
Heliotropium procumbens Mill. – LP 12280; Sub, SF
Heliotropium transalpinum Vell. – C 367; Sub, SF
Tournefortia rubicunda Salzm. ex DC. – LP 9978; Shrub, SF

Brassicaceae
Capparis brasiliana DC. – LP 9843, 12079; Shrub, SF
° *Capparis flexuosa* (L.) L. – LP 9930; C 302; Vine, SF
Capparis jacobinae Moric. ex Eichler – LP 9968; Shrub, SF
Capparis lineata Pers. – H 53483; LP 9934; C 271; Vine, SF
° *Crataeva tapia* L. – LP 12056; Tree, SF

Bromeliaceae
Aechmea aquilega (Salisb.) Griseb. – LP 12055; Herb, SF
Aechmea bromeliifolia (Rudge) Baker – C 295; Herb, ShF
Aechmea nudicaulis (L.) Griseb. – C 327; Epi, RF
Billbergia porteana Brongn. ex Beer – LP 9790; Epi, SF
Bromelia pinguin L. – Not collected, Herb, RF
Catopsis sessiliflora (Ruiz & Pav.) Mez – LP 10820; C 829; Epi, ShF
Cryptanthus bahianus L.B.Sm. – LP 9793; Herb, SF
Tillandsia polystachia (L.) L. – LP 10848; Epi, SF
Tillandsia stricta Sol. ex Sims – LP 10774, 10793; Epi, ShF
Tillandsia usneoides (L.) L. – Not collected, Epi, SF
Vriesea procera (Mart. ex Schult.f.) Wittm. – LP 12251, Herb, ShF
Vriesea simplex (Vell.) Beer – C 288, Epi, ShF

Burmanniaceae
Apteria aphylla (Nutt.) Barnhart ex Small – LP 10616; C 344; Herb, RF
Gymnosiphon divaricatum (Benth.) Benth. & Hook.f. – LP 10617; Herb, RF

Cactaceae
Brasiliopuntia brasiliensis (Willd.) Haw. – LP 9469; Tree, SF
Epiphyllum phyllanthus (L.) Haw. – C 332; Epi, SF
Pereskia aculeata Mill. – LP 10697; Tree, SF

Campanulaceae
Siphocampylus imbricatus G.Don – LP 12257, Shrub, ShF

Cannabaceae
° *Celtis iguanaea* (Jacq.) Sarg. – LP 9297, 9459; Tree, SF
Trema micrantha (L.) Blume – LP 12089; Tree, SF

Cannaceae
Canna glauca L. – C 814; Herb, RF

Celastraceae
Hippocratea volubilis L. – LP 9556; Vine, RF
Maytenus erythroxylon Reissek – LP 10654; C 784; Tree, SF
Maytenus quadrangulata (Schrad.) Loes. – LP 12042, 12113; C 789; Tree, SF
Tontelea nectandrifolia (A.C.Sm.) A.C.Sm. – LP 9890, 12065; C 234; Vine, SF

Chrysobalanaceae
Hirtella glandulosa Spreng. – LP 9539, 9776; Tree, RF, SF
Hirtella racemosa Lam. – LP 9544; C 315; Shrub, RF, SF

Clusiaceae
Clusia nemorosa G.Mey. – LP 9868; C 808, 827; Tree, RF, ShF

Combretaceae
Buchenavia capitata (Vahl) Eichler – LP 9780, 12252; Tree, RF, ShF

Commelinaceae
Commelina benghalensis L. – C 348; Herb, RF
* *Dichorisandra* sp. nov. – LP 12115; C 305; Herb, SF
Gibasis geniculata (Jacq.) Rohweder – LP 10797; Herb, ShF

Connaraceae
Connarus detersus Planch. – C 298; Tree, ShF
Rourea sp. – LP 12004; Shrub, RF
Rourea doniana Baker – LP 12109; C 291; Shrub, SF
Rourea martiana Baker – LP 9894; C 242; Vine, SF

Convolvulaceae
Evolvulus glomeratus Nees & Mart. – LP 9910; C 286; Sub, SF
Evolvulus latifolius Ker Gawl. – N 1027; C 331, 1218; Sub, SF
Ipomoea sp. – LP 10740; C 766; Vine, SF
Ipomoea hederifolia L. – LP 10736; Vine, SF
Ipomoea wrightii A.Gray – LP 12283; Vine, SF
Jacquemontia confusa Meisn. – C 384; Vine, SF
Jacquemontia densiflora (Meisn.) Hallier f. – C 9483; Vine, SF
Jacquemontia martii Meisn. – LP 9985; C 389; Vine, SF
Jacquemontia montana (Moric.) Meisn. – C 319; Vine, RF
Merremia cissoids (Lam.) Hallier f. – LP 10639; C 316; Vine, SF

Costaceae
Costus spiralis (Jacq.) Roscoe – LP 9871, 9775; Herb, RF, ShF

Cucurbitaceae
Anisosperma sp. – LP 12111; Vine, SF
Apodanthera sp. – C 380; Vine, SF
Apodanthera glaziovii Cogn. – LP 12064; Vine, SF
Cayaponia cf. *petiolulata* Cogn. – LP12069; Vine, SF

Gurania sp. – LP 12086; Vine, SF
Gurania subumbellata (Miq.) Cogn. – C 1247; Vine, SF
Psiguria triphylla (Miq.) C.Jeffrey – LP 10700; Vine, SF

Cunoniaceae
Lamanonia ternata Vell. – LP 9270, 12092; Tree, RF, SF

Cyperaceae
Cyperus cf. *compressus* L. – C 1255; Herb, SF
Cyperus laxus Lam. – C 372; Herb, SF
Rhynchospora cephalotes (L.) Vahl – LP 9430, 10826; Herb, RF, SF
Rhynchospora cf. *exaltata* Kunth – LP 9428; Herb, RF
Scleria bracteata Cav. – H 55452; Herb, RF
Scleria latifolia Sw. – H 55451; LP 9242; Herb, RF

Dilleniaceae
Doliocarpus sp. – LP 9537; Vine, RF

Dioscoreaceae
Dioscorea sp. – LP 9958; Vine, SF
Dioscorea altissima Lam. – LP 12088; Vine, SF
Dioscorea dodecaneura Vell. – LP 10711, 12279; Vine, SF

Ebenaceae
Diospyros inconstans Jacq. – LP 10007; C 256; Shrub, SF
Diospyros sericea A.DC. – LP 9247, 10849; Tree, RF, SF

Elaeocarpaceae
Sloanea guianensis (Aubl.) Benth. – LP 9504, 9782; Tree, RF

Eriocaulaceae
Paepalanthus spathulatus Körn. – LP 10768; Herb, ShF
Tonina fluviatilis Aubl. – LP 10754; Herb, RF

Erythroxylaceae
Erythroxylum macrocalyx Mart. – LP 9830, 9902, 12005; Tree, RF, SF
Erythroxylum polygonoides Mart. – LP 9936, 10720; C 355; Shrub, RF, SF

Euphorbiaceae
Acalypha amblyodonta (Müll.Arg.) Müll.Arg., Shrub, SF
Acalypha brasiliensis Müll.Arg. – LP 10006, 10683, 10799; Shrub, ShF, SF
Actinostemon concolor (Spreng.) Müll.Arg. – LP 9952; Shrub, SF
Actinostemon verticillatus (Klotzsch) Baill. – B 1239; Tree, SF
Alchornea triplinervia (Spreng.) Müll.Arg. – LP 10803; Tree, ShF
Bernardia tamanduana (Baill.) Müll.Arg. – LP 12047; C 1215; Shrub, SF
Cnidoscolus oligandrus (Müll.Arg.) Pax – LP 9451, 9408; Tree, SF
Cnidoscolus urens (L.) Arthur – LP 9995; Shrub, SF
Croton betulaster Müll.Arg. – LP 9265; Shrub, RF
Croton cordiifolius Baill. – LP 12041; C 262; Shrub, SF
Croton echioides Müll.Arg. – LP 9961; Shrub, SF
Croton hirtus L'Hér. – C 1256; Sub, SF
Croton lobatus L. – LP 9926; C 801; Shrub, RF, SF
Croton sincorensis Mart. ex Müll.Arg. – LP 9895; Shrub, SF
Croton tetradenius Baill. – LP 9295, 10662; Shrub, RF, SF
Croton triqueter Lam. – C 363; Sub, SF
Croton urticifolius Lam. – C 1222; Sub, SF
Croton velutinus Baill. – LP 9271; Shrub, RF
Croton warmingii Müll.Arg. – LP 10005; Shrub, SF
Dalechampia brasiliensis Lam. – LP 9986; Vine, SF
Dalechampia cf. *pentaphylla* Lam. – LP 9402; Vine, SF
Dalechampia scandens Vell. – LP 9903; Vine, SF
Dalechampia sylvatica S.Moore – LP 10674; C 802; Vine, SF
Euphorbia comosa Vell. – LP 10806; C 1267; Herb, ShF, SF
Euphorbia hyssopifolia L. – LP 9717 , Herb, SF
Euphorbia insulana Vell. – LP 10796; C 1285; Herb, ShF, SF
Jatropha palmatifolia Ule – LP 9933; Shrub, SF
Maprounea guianensis Aubl. – LP 9761, 9869, 12044; Tree, RF, SF
Manihot sp. – C 310; Tree, SF
Manihot cf. *anomala* Pohl – LP 9904; C 385, 782; Tree, SF
Manihot cf. *epruinosa* Pax & K. Hoffm. – LP 9387; Tree, SF
Pachystroma longifolium (Nees) I.M. Johnst. – LP 10659; Tree, SF
Pera glabrata (Schott) Poepp. ex Baill. – LP 12243; C 337, 342; Tree, RF, ShF
Philyra brasiliensis Klotzsch – L 259; Tree, SF
Richeria grandis Vahl – LP 10028; Tree, RF
Sebastiania corniculata (Vahl) Müll.Arg. – LP 10632; Shrub, RF
Tragia lessertiana (Baill.) Müll.Arg. – LP 9941, 12097, 12792; Vine, ShF, SF
Tragia volubilis L. – LP 10002; Vine, SF

Fabaceae-Caesalpinioideae
Apuleia leiocarpa (Vogel) J.F.Macbr. – LP 12063; C 809; Tree, SF
Bauhinia sp.1 – LP 9817; Shrub, SF
Bauhinia sp.2 – LP 12043; Vine, SF
Bauhinia forficata Link – LP 9815; Tree, SF
Bauhinia longifolia (Bong.) Steud. – LP 10753; C 364; Tree, SF
Bauhinia maximilianii Benth. – C 787; Vine, SF
Caesalpinia aff. *echinata* Lam. – LP 9405; Tree, SF
Caesalpinia leiostachya (Benth.) Ducke – C 1250; Tree, SF
Caesalpinia pluviosa DC. – LP 12264; Tree, SF
Cassia ferruginea (Schrad.) Schrad. ex DC. var. *ferruginea* – C 301; Tree, SF
Chamaecrista nictitans var. *pilosa* (Benth.) H.S.Irwin & Barneby – LP 9278; Sub, RF
Chamaecrista rotundifolia var. *grandiflora* (Benth.) H.S.Irwin & Barneby – LP 9833; C 236; Shrub, SF
Copaifera cearensis Huber ex Ducke – LP 9586; Tree, SF
Copaifera langsdorffii Desf. – LP 10625, 10756; Tree, RF, SF
Dimorphandra jorgei M.F.Silva – C 834; Tree, ShF
Goniorrhachis marginata Taub. – LP 9966; C 311; Tree, SF
° *Hymenaea courbaril* L. – C 768; Tree, SF
Melanoxylon brauna Schott – LP 10836; Tree, SF
Peltogyne confertiflora (Hayne) Benth. – LP 10779, 10831; Tree, ShF, SF
Peltogyne aff. *recifensis* Ducke – LP 12013; Tree, SF
° *Peltophorum dubium* (Spreng.) Taub. var. *dubium* – LP 9258; C 306, 243; Tree, RF, SF
* *Phanera trichosepala* L.P.Queiroz – LP 9413; C 281; Vine, SF
° *Poeppigia procera* var. *conferta* Benth. – LP 9914; C 257; Tree, SF

° *Pterogyne nitens* Tul. – H 53478; LP 10016; C 1239; Tree, SF
Schizolobium parahyba (Vell.) S.F.Blake – Not collected, Tree, SF
Senna acuruensis var. catingae (Harms) H.S.Irwin & Barneby – LP 9251, 9824; Shrub, SF
Senna acutisepala (Benth.) H.S.Irwin & Barneby – C 1270; Tree, SF
Senna aversiflora (Herb.) H.S.Irwin & Barneby – LP 10739, Shrub, SF
Senna hirsuta (L.) H.S.Irwin & Barneby – LP 10672, 10695; Shrub, SF
Senna macranthera var. *micans* (Nees) H.S.Irwin & Barneby – LP 9292; Tree, SF
Senna multijuga var. *verrucosa* (Vogel) H.S.Irwin & Barneby – LP 9555; Tree, SF
Senna pendula (Willd.) H.S.Irwin & Barneby – LP 9453, 9980; Shrub, SF
° *Senna spectabilis* var. *excelsa* (Schrad.) H.S.Irwin & Barneby – C 360; Tree, SF

Fabaceae-Mimosoideae
Albizia polycephala (Benth.) Killip ex Record – C 274; Tree, SF
Blanchetiodendron blanchetii (Benth.) Barneby & J.W.Grimes – LP 9813, 9984; Tree, SF
Inga edulis Mart. – LP 9302; C 374; Tree, SF
Inga aff. *laurina* Desv. – LP 9990; C 807; Tree, SF
Inga subnuda Salzm. ex Benth. subsp. *subnuda* – C 289; Tree, SF
Inga thibaudiana DC. subsp. *thibaudiana* – LP 10029; C 252; Tree, RF
Mimosa invisa Mart. ex Colla – LP 9277; Shrub, RF
Mimosa tenuiflora (Wild.) Poir. – LP 12242; Tree, SF
Piptadenia sp. – LP 9255, 12007; Vine, SF
Piptadenia adiantoides (Spreng.) Macbr. – LP 9825, 10713; Vine, SF
Piptadenia paniculata Benth. – H 53481; LP 10682; Tree, SF
Pseudopiptadenia bahiana G.P.Lewis & M.P.Lima – LP 9444, 12035; Tree, SF
Pseudopiptadenia contorta (DC.) G.P.Lewis & M.P.Lima – LP 12032; Tree, SF
Samanea inopinata (Harms) Barneby & J.G.Grimes – LP 9473; Tree, SF
Senegalia sp.1 – LP 12068; Tree, SF
Senegalia sp.2 – LP 10657; Vine, SF
Senegalia martiusiana (Steud.) Seigler & Ebinger – LP 10729; C 390; Shrub, SF
Senegalia riparia (Kunth) Britton & Killip – C 351; Tree, SF
Senegalia velutina (DC.) Seigler & Ebinger – C 382; Shrub, SF

Fabaceae-Papilionoideae
Aeschynomene elegans Schul. & Cham. var. *elegans* – LP 10688; Sub, SF
Aeschynomene histrix var. *densiflora* (Benth.) Rudd – LP 9293; Sub, SF
Andira fraxinifolia Benth. – LP 9284; Tree, RF
Bionia coriacea (Ness & Mart.) Benth. – LP 9272; Shrub, RF
Bowdichia virgilioides Kunth – LP 9781; Tree, RF
Canavalia parviflora Benth. – LP 12275; Vine, SF
Centrolobium tomentosum Guill. ex Benth. – H 53496; LP 9828; Tree, SF
Centrosema sagittatum (Humb. & Bonpl. ex Willd.) Brandegee – LP 9441, 10013; Vine, SF
Centrosema virginianum (L.) Benth. – LP 9974; Vine, SF
Chaetocalyx scandens var. *pubescens* (DC.) Rudd. – LP 9454; Vine, SF
Clitoria falcata Lam. – LP 9463; Vine, SF
Clitoria laurifolia Poir. – LP 10631; Sub, RF
* *Cratylia* sp. nov. – LP 10656; CO 15; Vine, SF
Crotalaria holosericea Nees & Mart. – LP 9426; C 322; Sub, SF
Crotalaria micans Link. – LP 10651; Sub, SF
Dalbergia decipularis Rizz. & Mattos – LP 12029; Tree, SF
Desmodium barbatum (L.) Benth. – C 800; Herb, SF
Desmodium incanum (Sw.) DC. – LP 10645; Herb, SF
Desmodium tortuosum (Sw.) DC. – LP 10644; Herb, SF
Desmodium uncinatum (Jacq.) DC. – C 1248, 1271; Herb, SF
Dioclea violacea Mart. ex Benth. – C 352; Vine, RF
Galactia striata (Jacq.) Urb. – LP 10687; C 359; Vine, SF
Indigofera suffruticosa Mill. – LP 9983; Sub, SF
Lonchocarpus cultratus (Vell.) A.M.G.Azevedo & H.C.Lima – LP 10010; Tree, SF
° *Machaerium acutifolium* Vogel – LP 9433, 10000; C 290; Tree, RF, SF
Macherium aff. *gracile* Benth. – LP 12020; Tree, SF
Machaerium hirtum (Vell.) Stellfeld – C 287; Tree, SF
Macroptilium erythroloma (Mart. ex Benth.) Urb. – LP 10640; C 371; Vine, SF
Myrocarpus fastigiatus Allemão – LP 12017; C 1230; Tree, SF
Periandra coccinea (Schrad.) Benth. – LP 9993; C 249; Vine, RF, SF
Platymiscium floribundum var. *obtusifolium* (Harms) Klitgaard – LP 9920; C 1251; Tree, SF
° *Platypodium elegans* Vogel – LP 10017, 10667; Tree, SF
Poiretia punctata Desv. – LP 10650; C 778; Vine, SF
Rhynchosia edulis Griseb. – LP 10641; Vine, SF
Rhynchosia melanocarpa Grear – LP 10671; Vine, SF
Rhynchosia phaseoloides (Sw.) DC. – LP 9924; Vine, RF
Rhynchosia reticulata var. *kuntzei* (Harms ex Kuntze) Grear – C 815; Vine, SF
Stylosanthes scabra Vogel – LP 10647; Herb, SF
Swartzia acutifolia Vogel – LP 9414, 9948; Tree, SF
Swartzia apetala Raddi var. *apetala* – LP 10015, 12073; Tree, SF
Vigna sp. – LP 10749, Vine, ShF
Vigna candida (Vell.) Maréchal, Mascherpa & Stainier – LP 12272; Vine, SF
Zollernia ilicifolia (Brongn.) Vogel – LP 12030; Tree, SF

Gentianaceae
Irlbachia purpurascens (Aubl.) Maas – LP 10634; Sub, RF
Voyria aphylla (Jacq.) Pers. – LP 10618; C 345; Herb, RF

Gesneriaceae
Nematanthus albus Chautems – LP 10782, Epi, ShF
* *Sinningia* sp. nov. – LP 12277, DC 2066, Herb, SF
Sinningia barbata (Nees & Mart.) G.Nicholson – LP 10795, Herb, ShF

Heliconiaceae
Heliconia pendula Wawra – C 1272; Shrub, ShF

Humiriaceae
Vantanea compacta (Schnizl.) Cuatrec. – LP 9921; C 361; Tree, RF

Iridaceae
Trimezia spathata subsp. *sincorana* (Rav.) Chukr – LP 9771; Herb, RF

Juncaceae
Juncus microcephalus H.B.K. – LP 10757; Herb, SF

Lamiaceae
Hyptis pectinata (L.) Poit. – LP 10765; Herb, SF
Hyptis sidifolia (L'Herit.) Briq. – LP 10003; Sub, SF
Hyptis suaveolens (L.) Poit. – LP 10638; C 362; Herb, SF
Ocimum campechianum Mill. – H 28446; LP 9997; Herb, SF
Salvia fruticetorum Benth. – H 53497; LP 10792; Sub, ShF, SF
Vitex aff. *klugii* Moldenke – LP 9946, 12015; C 283, 326; Tree, RF, ShF, SF

Lauraceae
Cinnamomum sp. – LP 10023; Tree, SF
Nectandra sp. – LP 12233; Tree, SF
Nectandra cf. *membranacea* (Sw.) Griseb. – H 53500; LP 10684; C 365; Tree, RF, SF
Ocotea glomerata (Nees) Mez – LP 12059; C 795; Tree, SF
Ocotea velutina (Ness) Rohwer – LP 10635; C 1292, 1290; Tree, RF, SF

Lecythidaceae
Cariniana estrellensis (Raddi) Kuntze – LP 10008; Tree, SF

Loganiaceae
Spigelia anthelmia L. – LP 9774; Herb, RF
Spigelia scabra Cham. & Schltdl. – LP 10750, 12081; Herb, ShF, SF
Strychnos sp. – LP 9965; C 388; Vine, SF
Strychnos brasiliensis Mart. – LP 9841; C 361; Vine, SF

Loranthaceae
Struthanthus polyrrhizus Mart. – LP 10685; Epi, SF

Lythraceae
Cuphea circaeoides Sm. ex Sims – LP 12282; Herb, SF
Cuphea impatientifolia A.St.-Hil. – LP 12226; Herb, SF
Cuphea racemosa (L.f.) Spreng. – LP 9560; C 813; Herb, RF, SF
Pleurophora anomala (A.St.-Hil.) Koehne – LP 12281; Sub, SF

Malpighiaceae
Bunchosia fluminensis Griseb. – LP 9912, 12049; Shrub, SF
Byrsonima sericea DC. – LP 9257, 9994/ 9385; Tree, RF, SF
Dicella bracteosa (A.Juss.) Griseb. – LP 9977; C 273; Vine, SF
Heteropterys aff. *fluminensis* (Griseb.) W.R.Anderson – LP 9942; Vine, SF
Heteropterys macrostachya A.Juss. – LP 10780; Vine, ShF, SF
Heteropterys perplexa W.R.Anderson – C 336; Vine, RF
Mascagnia sp. – C 811; Vine, SF
Mascagnia chasei W.R.Anderson – LP 9390; Vine, SF
Mascagnia rigida Griseb. – LP 10655; Vine, SF
Mascagnia sepium (A.Juss.) Griseb. – LP 9823; Vine, SF
Stigmaphyllon blanchetii C.E.Anderson – LP 9423, 9827; Vine, RF, SF
Tetrapterys sp.1 – LP 9947; Vine, SF
Tetrapterys sp.2 – CO 16; Vine, SF
Thryallis longifolia Mart. – C 235; Vine, SF

Malvaceae
Malvaceae sp. – LP 10840; C 779; Tree, SF
Bombacopsis stenopetala (Casar.) A.Robyns – LP 9291, 10819; Tree, ShF, SF
Cavanillesia arborea (Willd.) K.Schum. – C 2295; Tree, SF
Corchorus hirtus L. – LP 10646; Sub, SF
Eriotheca cf. *globosa* A. Robyns – LP 10030, 10776; Tree, RF, ShF
Eriotheca macrophylla (K.Schum.) A.Robyns – C 1237; Tree, SF
Guazuma ulmifolia Lam. – LP 9467; C 265; Tree, SF
Helicteres macropetala A.St.-Hil. – LP 10665; Shrub, SF
Luehea candicans Mart. – LP 9458, 9290; Tree, SF
Melochia betonicifolia A.St.-Hil. – LP 9938; C 366; Shrub, SF
Melochia tomentosa L. – LP 9450; Sub, SF
Pavonia malacophylla (Link & Otto) Garcke – LP 9509; Shrub, RF
Pavonia martii Colla – LP 9853; C 1286; Sub, SF
Sidastrum micranthum (A.St.-Hil.) Fryxell – LP 10642; Sub, SF
Waltheria indica L. – LP 9245; Sub, RF
Wissadula amplissima (L.) R.E.Fr. – LP 9443; C 771; Sub, SF
Wissadula contracta (Link) R.E.Fr. – LP 12238; Sub, SF

Marantaceae
Calathea sp. – LP 9929; Herb, RF
Maranta bicolor Ker Gawl. – LP 10698; Herb, SF
Maranta divaricata Roscoe – LP 9557; B 1260; Herb, RF, SF

Marcgraviaceae
Schwartzia brasiliensis (Choisy) Giraldo-Cañas – LP 12053; Vine, SF

Melastomataceae
Clidemia hirta (L.) D.Don – LP 10619; Shrub, RF
Henriettea succosa (Aubl.) DC. – C 300; Tree, RF
Leandra aurea (Cham.) Cogn. – LP 12093; Shrub, ShF
Miconia sp. – LP 9766; Shrub, RF
Miconia albicans (Sw.) Triana – LP 9866; Shrub, RF
Miconia aff. *caudigera* DC. – LP 9536; Tree, RF
Miconia ciliata (Rich.) DC. – LP 9866; Shrub, RF
Miconia mirabilis (Aubl.) L.O.Williams – LP 10628; C 246; Tree, RF
Miconia rimalis Naudin – LP 9533; Tree, RF
Pterolepis glomerata (Rottb.) Miq. – LP 9274, 10747; Sub, RF

Meliaceae
Trichilia sp. – LP 12046; Tree, SF
Trichilia emarginata (Turcz.) C.DC. – LP 9964; Tree, SF
Trichilia hirta L. – LP 12037; Tree, SF

Moraceae
Brosimum gaudichaudii Trécul – LP 9962; C 275; Tree, SF
Brosimum guianense (Aubl.) Huber – LP 12062; C 810; Tree, SF
* *Dorstenia caatingae* R.M. Castro – LP 10701; Herb, SF

Ficus citrifolia Mill. – LP 9468, 10813; C 349; Tree, RF, ShF, SF
Ficus cyclophylla (Miq.) Miq. – LP 12071; C 308; Tree, SF
Ficus gomelleira Kunth & C.D.Bouché – LP 12078; C 354; Tree, RF, ShF
Ficus pulchella Schott ex Spreng. – LP 12058; C 978; Tree, RF, SF
Maclura tinctoria (L.) D.Don ex Steud. – LP 9982; Tree, SF
Sorocea hilarii Gaudich. – LP 12057; Tree, SF

Myrsinaceae
Cybianthus sp. – C 1276; Tree, ShF
Myrsine ferruginea (Ruiz & Pav.) Spreng. – LP 10759; C 1246; Tree, ShF, SF
Myrsine guianensis (Aubl.) Kuntze – LP 9286; C 350; Tree, RF
Myrsine venosa A.DC. – LP 10764, 12245; Tree, ShF

Myrtaceae
Eugenia sp.1 – C 772, 777; Shrub, SF
Eugenia sp.2 – LP 9991; Shrub, SF
Eugenia sp.3 – LP 12045; Tree, SF
* *Eugenia* sp. nov. – LP 10727; C 393, 1487; Tree, SF
Eugenia cf. *candolleana* DC. – LP 10723; Tree, SF
Eugenia florida DC. – C 2041; Tree, SF
Eugenia punicifolia (Kunth) DC. – LP 9283, 9796; Shrub, RF, SF
Myrcia sp.1 – C 245, 391; Tree, SF
Myrcia sp.2 – C 341; Shrub, SF
Myrcia sp.3 – LP 9949; Shrub, SF
Myrcia blanchetiana (O.Berg.) Mattos – LP 12104; Tree, ShF
Myrcia guianensis (Aubl.) DC. – LP 9959, 12006; Tree, RF, SF
Myrcia rostrata DC. – LP 9762; Tree, RF
Myrcia splendens (Sw.) DC. – LP 12009, 12074; Shrub, RF, ShF
Myrciaria floribunda (H.West ex Willd.) O.Berg – LP 10703; C 774; Tree, SF
Psidium sp. – LP 12026; Shrub, SF
Psidium cf. *brownianum* DC. – LP 12033, 12096; Tree, ShF, SF
Psidium schenckianum Kiaersk. – C 330; Shrub, SF

Nyctaginaceae
Bougainvillea spectabilis Willd. – C 263; Vine, SF
Guapira hirsuta (Choisy) Lundell – LP 9972; Tree, SF
Guapira opposita (Vell.) Reitz – LP 10009, 12080; C 1279; Tree, ShF, SF

Ochnaceae
Sauvagesia erecta L. – LP 10627; Herb, RF

Olacaceae
Heisteria blanchetiana (Engler) Sleumer – LP 12098; Tree, ShF
Schoepfia brasiliensis A.DC. – LP 9542, 10769; Tree, RF, ShF
Ximenia americana L. var. *americana* – LP 10775; C 266, 1238; Tree, ShF, SF

Orchidaceae
Bulbophyllum sanderianum Rolfe – C 312; Epi, RF
Campylocentrum micranthum (Lindl.) Rolfe – LP 9535; Epi, RF
Cleistes metallina (Barb. Rodr.) Schltr. – LP 10630; Herb, RF
Cleistes pluriflora (Barb. Rodr.) Schltr. – LP 12256; Herb, ShF
Dichaea cogniauxiana Schltr. – C 1269; Herb, ShF
Eltroplectris calcarata (Sw.) Garay & H.R.Sweet – LP 9424; Herb, RF
Eltroplectris triloba (Lindl.) Pabst – LP 9424; Herb, RF
Eurystylis actinosophila (Barb. Rodr.) Schltr. – LP 10823; Epi, ShF
Galeandra beyrichii Rchb. f. – H 53499; LP 9506; Herb, RF, SF
Maxillaria sp. – C 1297; Epi, SF
Notylia hemitricha Barb. Rodr. – LP 9464; Epi, SF
Oeceoclades maculata (Lindl.) Lindl. – LP 9438; Herb, RF
Oncidium ciliatum Lindl. – LP 10798; Epi, ShF
Oncidium flexuosum (Kunth) Lindl. – LP 10785, Epi, ShF
Pogoniopsis schenkii Cogn. – LP 12255, Herb, ShF
Polystachya estrellensis Rchb.f. – LP 10808; Epi, ShF
Prescottia oligantha Lindl. – LP 9534; Herb, RF
Prosthechea aemula (Lindl.) W.E.Higgins – C 1295; Epi, SF
Psilochilus cf. *modestus* Barb. Rodr. – LP 9507; Herb, RF
Rauniella sp. – S 674; Epi, ShF
Scaphyglottis modesta Schltr. – LP 10818; Epi, ShF
Sobralia sessilis Lindl. – H 55461; LP 10791; Herb, ShF
Stelis sp. – LP 10812; Epi, ShF
Wullschlaegelia calcarata Benth. – LP 10767; Herb, ShF

Oxalidaceae
Oxalis barrelieri L. – H 53498; LP 12225; Sub, SF
Oxalis neuwiedii Zucc. – LP 9988; C 1262; Herb, SF
Oxalis roselata A.St.-Hil. – LP 10699; Herb, SF

Passifloraceae
Passiflora alata Dryander – LP 10622; Vine, RF
Passiflora bahiensis Klotzsch – LP 10675, 12235; Vine, SF
Passiflora cincinnata Mast. – C 314, 1268; Vine, SF
Passiflora edulis Sims – LP 9875; Vine, SF
Passiflora galbana Mast. – LP 9305, 10623; C 1281; Vine, RF, ShF, SF
Passiflora organensis Gardner – LP 9288; Vine, SF
Passiflora setacea DC. – LP 10011, 9907; Vine, SF
Passiflora suberosa L. – C 1244; Vine, SF

Phyllanthaceae
* *Astrocasia jacobinensis* (Müll.Arg.) G.L.Webster – C 1235; Tree, SF
Phyllanthus sp. – LP 12117; Herb, SF
Phyllanthus niruri L. – C 1259; Herb, SF

Phytolaccaceae
Gallesia integrifolia (Spreng.) Harms – C 1257; Tree, SF
Microtea paniculata Moq. – LP 12083; Herb, ShF, SF
Rivina humilis L. – LP 10648; Shrub, SF
Seguieria floribunda Benth. – LP 12261; Vine, SF

Piperaceae
Peperomia sp. – C 294; Epi, ShF
Peperomia cf. *glabella* (Sw.) A.Dietr. – LP 9460, 10708; Herb, SF
Piper aduncum L. – LP 9559; Shrub, RF
Piper amalago L. – LP 10004; Shrub, SF
Piper arboreum Aubl. var. *arboreum* – LP 9241, 9466; C 793; Shrub, RF, SF

Plumbaginaceae
Plumbago scandens L. – LP 12266, Herb, SF

Poaceae
Poaceae sp. – LP 9243; Herb, RF
Ichnanthus bambusiflorus (Trin.) Döll – H 55450; Herb, SF
Ichnanthus grandifolius (Döll) Zuloaga & Soderstr. – H 53510; Herb, ShF
Ichnanthus pallens (Sw.) Munro ex Benth. – LP 9783; Herb, RF
Olyra latifolia L. – LP 12231; Herb, SF
Parodiolyra micrantha (Kunth) Davidse & Zuloaga – LP 9429, 9927; Herb, RF
Raddia portoi Kuhlm. – DC 2063; Herb, SF
Streptostachys asperifolia Desv. – LP 12019; Herb, SF

Polygalaceae
Bredemeyera martiana A.W.Benn. – LP 10844; Vine, SF
Polygala mollis Kunth – LP 9540; Herb, RF
Polygala paniculata L. – H 55457; Herb, SF
Polygala urbani Chodat – LP 9279, 9975; Sub, RF, SF
Polygala violacea Aubl. – LP 9897; Sub, SF
Securidaca diversifolia (L.) S.F.Blake – LP 9842, 9893; Vine, SF
Securidaca lanceolata A.St.-Hil. & Moq. – LP 9870; Vine, RF

Polygonaceae
Coccoloba alnifolia Casar. – LP 1071; C 1260; Tree, SF
Coccoloba declinata (Vell.) Mart. – LP 12031; C 1253; Vine, SF

Portulacaceae
Talinum paniculatum (Jacq.) Gaertn. – LP 9461; Herb, SF
Talinum triangulare (Jacq.) Willd. – C 1266, Herb, SF

Proteaceae
Roupala montana Aubl. – LP 9514, 9923; Tree, RF, ShF

Rafflesiaceae
Pilostyles blanchetii (Gardner) R.Br. – H 53495; Epi, SF

Rhamnaceae
° *Ziziphus joazeiro* Mart. – LP 9831; Tree, SF

Rubiaceae
° *Alseis floribunda* Schott – LP 9905; Tree, SF
Amaioua guianensis Aubl. – C 323, 1164; Shrub, RF, SF
Borreria latifolia (Aubl.) K.Schum. – LP 10744; Herb, SF
Chiococca alba (L.) Hitchc. – H 53493; LP 12087; Shrub, SF
Chomelia sp. – LP 12114; Tree, SF
Coccocypselum sp. – LP 10629; C 251; Herb, RF
° *Coutarea hexandra* (Jacq.) K.Schum. – LP 10817; C 1165; Tree, ShF, SF
Declieuxia fruticosa (Willd. ex Roem. & Schult.) Kuntze – LP 9260,10834; C 248; Herb, RF, SF
Diodella apiculata (Willd. ex Roem. & Schult.) Bacigalupo & E.L.Cabral – LP 10741; Sub, SF
Emmeorhiza umbellata (Spreng.) K.Schum. – LP 10846; Vine, SF
Faramea hyacinthina Mart. – LP 9956; Shrub, SF
Hamelia patens Jacq. – LP 10021; C 373; Shrub, SF
Manettia cordifolia Mart. – LP 10676; Vine, SF
Mitracarpus frigidus K.Schum. – LP 10761; Sub, SF
Mitracarpus hirtus (L.) DC. – LP 10742; Herb, SF
Molopanthera paniculata Turcz. – LP 9285; Tree, SF
Palicourea blanchetiana Schltdl. – LP 9864, 9760, 10621; Shrub, RF
Margaritopsis carrascoana (Delprete & E.B.Souza) C.M.Taylor & E.B.Souza – LP 9953; Shrub, SF
Psychotria carthagenensis Jacq. – LP 9246, 10614; Shrub, RF
Psychotria chaenotricha DC. – LP 12034; C 264, 261; Shrub, SF
Psychotria hoffmannseggiana (Willd. ex Roem. & Schult.) Müll. Arg. – LP 10633; Shrub, RF
Randia armata (Sw.) DC. – LP 10704; Tree, SF
* *Spermacoce* sp. nov. – LP 10828; C 1294; Herb, SF
* *Standleya* sp. nov. – LP 10835; C 764; Herb, SF

Rutaceae
Almeidea rubra A. St.-Hil. – LP 10706; C 303; B 1261; Shrub, SF
Angostura bracteata (Nees & Mart.) Kallunki – LP 9844, 10653; Shrub, SF
* *Conchocarpus* sp. nov. – LP 9845, 10845; C 392, Shrub, SF
Conchocarpus heterophyllus (A.St.-Hil.) Kallunki & Pirani – H 28448; LP 9908; C 769; Shrub, SF
Conchocarpus macrophyllus J.C.Mikan – C 786; Shrub, SF
Dictyoloma vandellianum A.Juss. – LP 9547; Tree, RF, SF
Esenbeckia grandiflora Mart. subsp. *grandiflora* – C 785; Tree, SF
Esenbeckia leiocarpa Engl. – C 780; Tree, SF
Helietta glaziovii (Engl.) Pirani – LP 12052; Tree, SF
Pilocarpus riedelianus Engl. – LP 9791, 12067; Shrub, SF
Pilocarpus spicatus A.St.-Hil. subsp. *spicatus* – LP 10658; C 836; Tree, SF
Zanthoxylum acuminatum (Sw.) Sw. – C 267, 783; Tree, SF
Zanthoxylum cf. *nigrum* Mart. – C 1233; Tree, SF
Zanthoxylum rhoifolium Lam. – LP 10624; Tree, RF
Zanthoxylum tingoassuiba A.St.-Hil. – C 1486; Tree, SF

Salicaceae
Casearia arborea (Rich.) Urb. – H 53489; Tree, SF
Casearia javitensis Kunth – LP 9891; C 334; Shrub, RF, SF
Casearia sylvestris Sw. – LP 12110; C 776; Tree, SF

Sapindaceae
Allophylus cf. *laevigatus* Radlk. – LP 12050; C 307, 1234; Shrub, SF
Allophylus sericeus (Cambess.) Radlk. – H 53488; LP 12070, Tree, SF
Averrhoidium gardnerianum Baill. – LP 9809; Tree, SF
Cardiospermum corindum var. *elongatum* (Radlk.) F.A.Barkley – LP 10020; Vine, SF
Cupania rigida Radlk. – LP 9455, 9835, 10841; Tree, RF, SF
Paullinia elegans Cambess. – LP 10670; Vine, SF
Paullinia racemosa Wawra – LP 10842; Vine, SF
Paullinia revoluta Radlk. – C 773; Vine, SF
Serjania sp. – LP 9386; C 386; Vine, SF
Serjania fuscifolia Radlk. – LP 9384, 10719; Vine, SF
Serjania pernambucensis Radlk. – LP 9249, 12190; Vine, SF
Thinouia sp. – LP 9439; C 1245; Vine, SF
Urvillea laevis Radlk. – LP 9449; Vine, SF
Urvillea ulmacea Kunth – LP 9259, 9388; Vine, RF, SF

Sapotaceae
Chrysophyllum gonocarpum (Mart. & Eichler ex Miq.) Engl. – LP 9298; C 788; Tree, SF

Chrysophyllum rufum Mart. – LP 12048; Tree, SF
Manilkara rufula (Miq.) H.J.Lam – LP 12054; Tree, ShF, SF
Pouteria sp.1 – LP 9452; Tree, SF
Pouteria sp.2 – LP 9407, 12112; Tree, SF
Pouteria ramiflora (Mart.) Radlk. – LP 9772; C 233, 775; Tree, RF, SF

Simaroubaceae
Simarouba amara Aubl. – LP 9303; Tree, SF

Smilacaceae
Smilax sp. – C 370; Vine, SF

Solanaceae
° *Brunfelsia uniflora* (Pohl) D.Don – H 53494; Tree, SF
Cestrum gardneri Sendtn. – LP 10702; Tree, SF
Cestrum laevigatum Schltdl. – LP 10024; Shrub, SF
Dyssochroma viridiflora Miers – LP 10777; Vine, ShF
Heteranthia decipiens Nees & Mart. – LP 10710; Herb, SF
Metternichia princeps Mik. – LP 9287; C 258; Shrub, SF
Schwenkia americana L. – LP 10745; Sub, SF
* *Solanum* sp. nov. – LP 10850; Shrub, SF
Solanum caavurana Vell. – C 377; Shrub, SF
Solanum crinitum Lam. – LP 9549; Shrub, SF
Solanum depauperatum Dunal – LP 10801; Shrub, ShF
Solanum jabrense Agra & M.Nee – LP 9432, 10014, 10838; Shrub, RF, SF
Solanum palinacanthum Dunal – LP 12236; Sub, SF
Solanum paniculatum L. – B 1237; Shrub, SF

Styracaceae
Styrax camporum Pohl – LP 3541; C 335; Shrub, RF, SF

Trigoniaceae
Trigonia bahiensis E.F.Guimar., Miguel & Fontella – LP 9937, 10660; C304; Vine, SF
Trigonia eriosperma (Lam.) Fromm & E.Santos – C 781; Shrub, SF
Trigonia nivea Cambess. var. *nivea* – LP 9957; C 282; Vine, SF
Trigonia nivea var. *pubescens* (Cambess.) Lleras – LP 9252, 9798, 9874; Vine, SF

Turneraceae
Turnera cearensis Urb. – H 53491; LP 9922; C 1220; Shrub, SF

Urticaceae
Cecropia pachystachya Trécul – LP 9770; RC 1031; Tree, RF, SF
Urera caracasana (Jacq.) Gaudich. ex Griseb. – LP 12076; Tree, SF
Urera nitida (Vell.) Brack – LP 9465; Shrub, SF

Verbenaceae
Aloysia virgata (Ruiz & Pav.) Juss. – LP 9834; Shrub, SF
Lantana camara L. – LP 9859; C 1212; Shrub, SF
Lantana canescens Kunth – LP 12240; Shrub, SF
Lantana fucata Lindl. – LP 10726; Sub, SF

Violaceae
Anchietea selloviana Cham. & Schltdl. – C 279; Shrub, SF
Hybanthus atropurpureus (A.St.-Hil.) Taub. – H 53479; Shrub, SF
Hybanthus calceolaria (L.) Schulze-Menz – C 379; Herb, SF

Viscaceae
Phoradendron crassifolium (Pohl ex DC.) Eichler – C 293; Epi, SF
Phoradendron mucronatum (DC.) Krug & Urb. – LP 10847; C 329; Epi, SF
Phoradendron perrottetii (DC.) Eichler – LP 9550; C 328; Epi, RF
Phoradendron cf. *pteroneuron* Eichler – LP 12066; Epi, SF

Vitaceae
Cissus albida Cambess. – C 250; Vine, RF

Vochysiaceae
Vochysia sp. – Not collected, Tree, ShF

Xyridaceae
Xyris jupicai Rich. – LP 10755; Herb, SF

PTERIDOPHYTES

Aspleniaceae
Asplenium auriculatum Sw. – LP 12102; Herb, ShF
Asplenium serra Langsd. & Fisch. – LP 10766; Herb, ShF

Cyatheaceae
Cyathea delgadii Sternb. – LP 9263; Tree, RF

Dennstaedtiaceae
Lindsaea lancea (L.) Bedd. – LP 9512; Herb, RF
Lindsaea stricta (Sw.) Dryand. – LP 9545; Herb, RF

Dryopteridaceae
Ctenitis submarginalis (Langsd. & Fisch.) Ching – C1273; Herb, ShF

Lycopodiaceae
Lycopodiella cernua (L.) Pic. Serm. – C 804; Sub, SF

Polypodiaceae
Niphidium crassifolium (L.) Lellinger – LP 10805; Herb, ShF
Microgramma geminata (Schrad.) Presl – LP 9792, Epi, SF
Microgramma squamulosa (Kaulf.) de la Sota – LP 10814; Epi, ShF
Polypodium catharinae Langsd. & Fisch. – C 831; Epi, ShF
Polypodium triseriale Sw. – LP 10815; Herb, ShF

Pteridaceae
Doryopteris lomariacea Kl. – LP 9398; Herb, SF

Schizaeaceae
Anemia cf. *filiformis* Sw. – LP 12267; Herb, SF
Anemia hirsuta (L.) Sw. – LP 9289; Herb, SF
Schizaea elegans (Vahl) Sm. – LP 9266; Herb, RF

Selaginellaceae
Selaginella muscosa Spring – LP 10809; Herb, ShF

Thelypteridaceae
Thelypteris salzmannii (Fée) C.V.Morton – LP 9472; Herb, SF

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BOOK NOTICE

Ana Cláudia Araújo, Edgley A. César, and David Simpson. 2007. **Preliminary List of the Cyperaceae in Northeastern Brazil: Repatriation of Kew Herbarium Data for the Flora of Northeastern Brazil Series, vol. 3.** (ISBN 978-1-84246-204-1, pbk.). Royal Botanic Gardens, Kew, Richmond, Surrey, TW9 3AB, United Kingdom. (**Orders:** www.kewbooks.com, publishing@kew.org). $51.55, 32 pp., 11 3/4" × 8 1/4".

Contents:

Texto em Português
Mapa de densidade de espécies/Species density map
Bibliografia/References
Text in English
Listagem/Checklist
Lista de Exsicatas/List of Specimens

This is a straightforward checklist of the Cyperaceae of Northeastern Brazil, presented in both Portuguese and English text, with a Forward by Wm. Wayt Thomas of The New York Botanical Garden. From the publishers: "Between 2002 and 2004, 1932 Cyperaceae specimens were examined and the information repatriated. This checklist records 191 species and 24 genera, with entries listed alphabetically and sorted by state, collector and number. An additional exsiccatae list enables duplicates lodged in other herbaria to be checked against the correct determination."

DIVERSITY AND FLORISTIC COMPOSITION OF THE VASCULAR PLANTS IN THE FOREST FRAGMENT IN SOUTHEASTERN RIO DE JANEIRO, BRAZIL

Regina H.P. Andreata
Universidade Santa Úrsula/ICBA
22231-040, R. Fernando Ferrari 75,
RJ, BRASIL
regina.andreata@gmail.com

Haroldo C. de Lima
Instituto de Pesquisas
Jardim Botânico do Rio de Janeiro
22460-030; R. Pacheco Leão 915, RJ, BRASIL
hlima@jbrj.gov.br

Angela S. Fonseca Vaz
IBGE/Instituto de Pesquisas
Jardim Botânico do Rio de Janeiro
22460-030, R. Pacheco Leão 915, RJ, BRASIL
avaz@jbrj.gov.br

José Fernando A. Baumgratz
Instituto de Pesquisas
Jardim Botânico do Rio de Janeiro
22460-030, R. Pacheco Leão 915, RJ, BRASIL
jbaumgra@jbrj.gov.br

Sheila R. Profice
Instituto de Pesquisas Jardim Botânico do Rio de Janeiro
22460-030, R. Pacheco Leão 915, RJ, BRASIL
sprofice@jbrj.gov.br

ABSTRACT

The diversity and floristic composition of the vascular plants of the Morro Alto Mourão, within the Serra da Tiririca State Park, Rio de Janeiro State, Brazil (22° 58' 04" S x 43° 01' 17" W), were analyzed. The study area includes an important fragment of montane forest within the Atlantic Coastal Forest biome. A total of 369 taxa were collected, including 7 Pteridophytes, 295 Dicotyledons, and 67 Monocotyledons, belonging to 84 different families. These plants are distributed among three life-forms: arboreal, shrub-arboreal, and herbaceous. A map of the area, a graphic representation of the local water balance, plant profiles, soil analyses and descriptions of the climates of the eastern and western facing slopes of the Serra da Tiririca Mountains are presented. Rare or endangered and endemic species are indicated. A list of the taxa is also provided that cites flowering and fruiting, habit descriptions in addition to the name of the collectors.

RESUMO

A diversidade e a composição florística das plantas vasculares foram analisadas no Morro Alto Mourão (22° 58' 04" S e 43° 01' 17" W) situado no Parque Estadual da Serra da Tiririca, localizado no estado do Rio de Janeiro, Brasil. A área de estudo compreende um importante fragmento florestal da cadeia montanhosa litorânea que integra a Mata Atlântica. Foram registrados 369 táxons, sendo 7 Pteridófitas, 295 Dicotiledôneas e 67 Monocotiledôneas, pertencentes a 84 famílias. As plantas distribuem-se em três formações: arbórea, arbustivo-arbórea e herbácea. Apresenta-se um mapa, gráficos de balanço hídrico e perfis esquemáticos da área. São dadas informações referentes à análise do solo. Caracterizam-se os tipos climáticos das encostas voltadas para oeste e a leste da Serra da Tiririca. Assinala-se a ocorrência de espécies raras e/ou ameaçadas e endêmicas. É fornecida uma listagem dos táxons, dados do hábito, floração, frutificação e dos coletores do material examinado.

INTRODUCTION

Coastal forests are an important component of the Atlantic Coastal Forest biome. These forests are distributed along most of the eastern coast of Brazil. However, they have been subject to intense degradation within this range, due mainly to their proximity to large urban centers.

Detailed information concerning the coastal vegetation of Rio de Janeiro State is relatively limited. This study examines the coastal vegetation of the Morro Alto Mourão region, including components of the humid coastal forest and the near-shore (*restinga*) vegetation. The Morro Alto Mourão is one of the highest points in the Serra da Tiririca Range (369 m). It is located in southeastern Rio de Janeiro State between the municipalities of Niterói and Maricá. It still retains significant fragments of one of the most highly threatened biomes in the world—the Atlantic Coastal Forest.

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The Serra da Tiririca Range is oriented almost perpendicular to the Atlantic coastline, which results in contrasting climatic conditions on its two flanks. The western slopes are generally exposed to the humid ocean winds. Intense rainfall is also common, principally due to cold fronts arriving from the southern polar region. On the other hand the more sheltered eastern slopes lie in the rain shadow and receive less and lighter rainfall.

The first historical references to the area date from the end of the 16th century when the Portuguese crown awarded a large land title (*sesmaria*) to Duarte Martins Mourão. This title granted formal control of the coastal lands between the Lagoa de Piratininga and Pedra de Inoã, in the current municipality of Maricá. Human use and occupation of this region is very intense. It was cultived with large numbers of small sugar cane, coffee, and banana plantations, as well as citrus orchards up until the start of the 20th century (Grael et al. 1995).

Even though this region was highly disturbed (and is located near large urban centers as Niterói and Maricá cities) the vegetation on the Morro Alto Mourão is experiencing a gradual but natural regeneration. Currently, plants with ornamental, medicinal, timber value and species of great scientific importance (rare or endemic to the State of Rio de Janeiro and/or the Atlantic Coastal Forest) that are often little known to botanists have been discovered.

Preliminary data from this study have been presented at scientific meetings and helped transform the Serra da Tiririca Environmental Protection Area into the more highly protected Serra da Tiririca State Park (Rio de Janeiro State Law No.1901, of November 29, 1991).

This study presents the results of a floristic inventory undertaken in the area around the Morro Alto Mourão. This inventory examined the diversity and composition of the vascular plants within an area of coastal forest. It is intended to be used to support conservation and degraded areas restoration efforts along Rio de Janeiro State coast.

MATERIALS AND METHODS

Study Area

The Morro Alto Mourão is located in the Serra da Tiririca Range, which covers a approximately 2700 hectares near Pontas de Itaipuaçu and Itacoatiara (22° 58' 04" S × 43° 01' 17" W) (Fig. 1). The Morro Alto Mourão is part of a pre-Cambrian age crystalline massif (Niterói Massif) located along the eastern shore of the Guanabara Bay. The peak has one of the highest elevations (369 m) in the Tiririca mountains, together with Morro do Elefante (or Falso Pão-de-Açúcar) (412 m) and Morro do Telégrafo (250 m) (Pontes 1987).

The ground is generally covered by leaf litter although there are also exposed rock areas. The sandy-clay soil has a medium texture, is highly acidic (pH = 4.7–4.8) and has mid-range quantities of calcium (3.5 me/100 mg), phosphorous (12 ppm) and magnesium (1.6 me/100 mg). The aluminum concentration is high (1.0 me/100 mg), and the potassium concentration very high (> 135 ppm). The high acidity and large quantities of aluminum and potassium found in the soils are probably the result of leaching and frequent burning.

The western slopes of the Tiririca Range have a sub-humid climate (C2), with an A' megathermic temperature regime. The average annual temperature is 23.2° C, annual rainfall 1305 mm, annual evapo-transpiration potential 1271 mm, real annual evapo-transpiration 1207 mm, annual water-deficit 64 mm and annual excess 98 mm (Fig. 2). On the other hand, the eastern slopes have a sub-humid humid climate (C2) and a B4 meso-thermic temperature regime.

The average annual temperature there is 23.2° C, annual rainfall 1207 mm, annual evapo-transpiration potential 1223 mm, real annual evapo-transpiration 1163 mm, annual water-deficit 60 mm and annual excess 62 mm (Fig. 3). The greater rainfall and humidity encountered on the western slopes are due to the direct influence of humid on-shore ocean winds.

Methods

Plant collections were made during systematic monthly excursions to the area between 1980–85 and 1989–90.

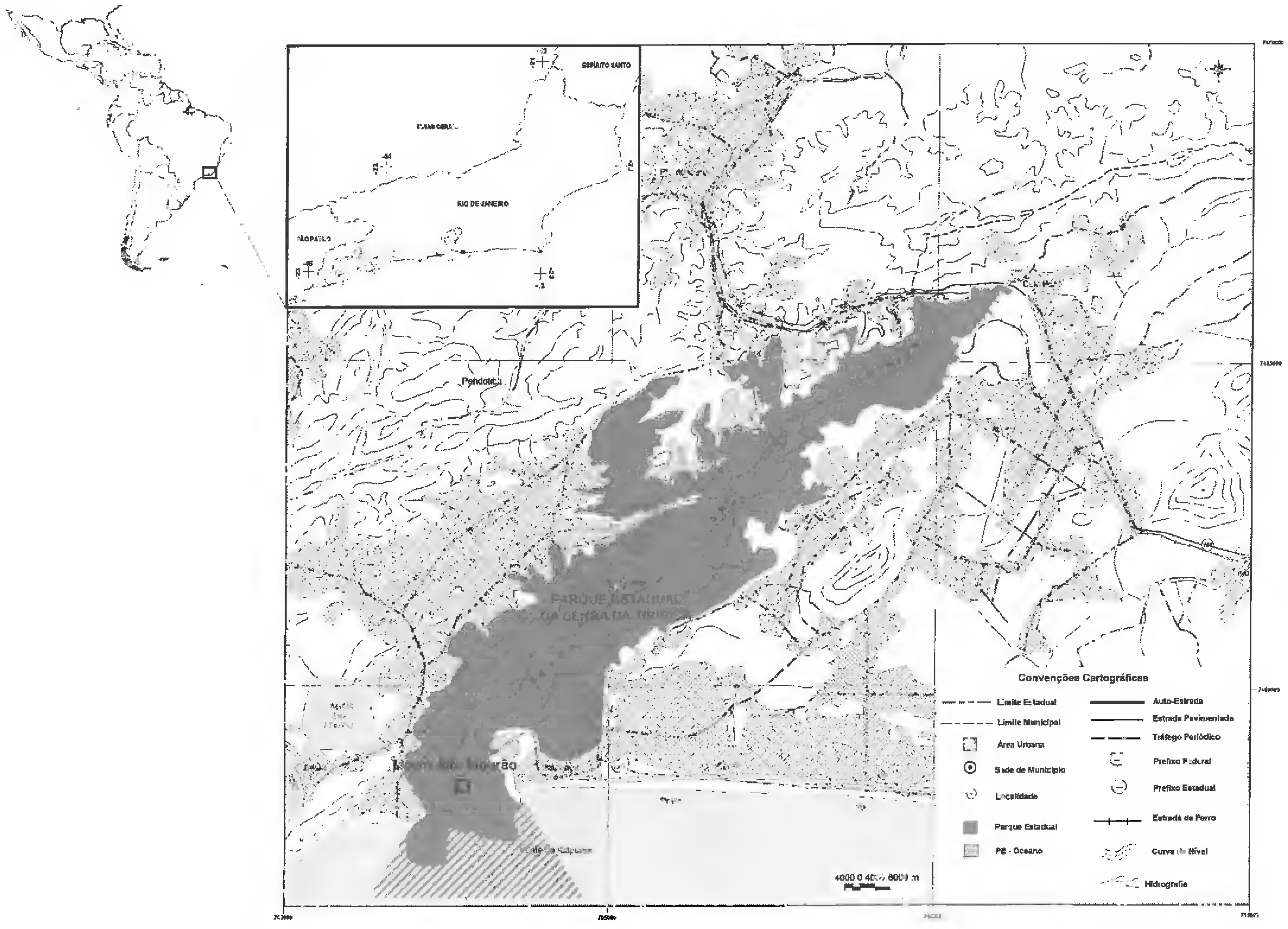

Fig. 1. Localization of the Morro Alto Mourão, Rio de Janeiro State, Brazil.

Collections were undertaken on the Morro Alto Mourão, as well as on the Morro do Elefante and Pedra de Itacoatiara, which have a similar vegetation cover. During the period from 1986 to 1988, collections were less frequent. However, these were generally accompanied by certain plant group specialists or undertaken especially to prepare schematic diagrams representing the phytophysiognomy of the vegetation.

All collected material was identified and registered at the herbaria of the Instituto de Pesquisas Jardim Botânico do Rio de Janeiro (RB), the Universidade Santa Úrsula (RUSU) and GUA, HB, FFP (Orchidaceae).

The plant lists are presented in an appendix, with the family names in alphabetical order. The Angiosperm families are named according to Cronquist (1988). Those of the Pteridophytes are named according to Kramer and Green (1990). The flowering and fruiting periods are derived from the specimens collected in the area.

A map of the area, diagrams indicating the water balance and schematic vegetation profiles are provided. The different phytophysiognomies were classified as either arboreal, shrub-arboreal, or herbaceous in order to characterize the vegetation cover.

Climatic data for the Serra da Tiririca was obtained from the Niterói Weather Station (representing the climatic conditions prevalent on the western slopes, directly exposed to humid winds and intense rainfall) and from the Maricá Station (representing the climatic conditions prevalent on the eastern slopes that are shielded from the humid winds and intense rainfall characteristic of the western slopes). The techniques of Thornthwaite and Mather (1955) were employed to prepare local water balance diagrams, quantify the available soil humidity (evapo-transpiration) and determine the degree (either deficiency or surplus) of the water balance during the year based on the monthly rainfall data obtained from these stations.

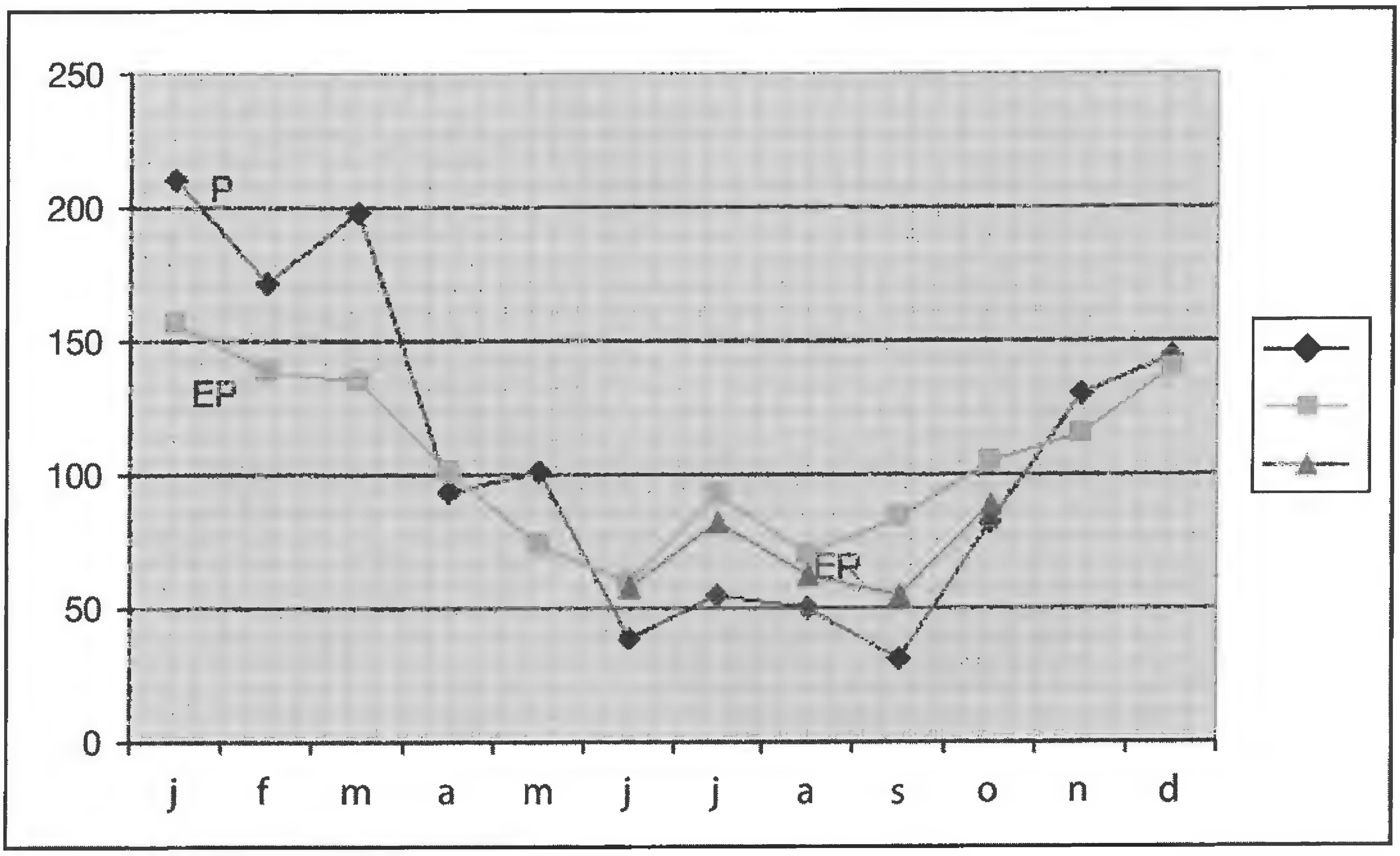

Fig. 2. Diagram of the water balance of Niterói (1958–67). Water Balance according to Thornthwaite & Mather (1955). Latitude: 22° 54'S- Longitude: 43° 07'W. Annual Precipitation: 1305 mm = P. Annual Evapo-transpiration potential: 1271 mm = EP. True Annual Evapo-transpiration: 1207 mm = ER. Annual Water deficit: 64 mm. Annual Water Excess: 98 mm.

Two soil samples were taken (0–20cm deep) and analyzed at The Soil Fertility Division of the National Service of Research and Conservation of Soils at EMBRAPA, in the city of Rio de Janeiro.

RESULTS AND DISCUSSION

Taxonomic diversity

A total of 369 taxa were sampled within the study area. Seven of those were Pteridophytes (3 families), 295 were Dicotyledoneae (63 families) and 67 Monocotyledoneae (18 families) (Appendix 1).

Leguminosae (40 taxa), Euphorbiaceae (23), Rubiaceae (20), Myrtaceae (15), Solanaceae (16), Bromeliaceae (12), Orchidaceae (12), Araceae (11) and Sapindaceae (11) represented the greatest taxa richness. These totaled 43% of the Angiosperms encountered.

Solanum (10 taxa), *Rhipsalis* (6), *Machaerium*, *Philodendron*, *Anthurium* and *Trichilia* (5 taxa each) were the most representative genera.

Classifying these plants by habit, the largest diversity was observed among the herbs and sub-shrubs, which were regionally represented by 115 taxa. The trees comprised 96 taxa, followed by the shrubs, climbers and epiphytes, with 92, 52, and 18 taxa, respectively (Appendix 1).

Comparisons of the plant species richness of Morro do Alto Mourão with other forest areas within the Serra do Mar Range in Rio de Janeiro State are shown in Table 1. A tendency towards reduced species richness can be seen within coastal forest areas near the city of Rio de Janeiro (Morro do Alto Mourão, Horto/JBRJ, and Morro das Andorinhas) in relation to humid forests in the Serra do Mar Range (Macaé de Cima, Cairuçu, and Tinguá). However, the high degree of local endemism of the coastal forests is very notable, with 20 species restricted to only Rio de Janeiro State (Appendix 1). This same pattern of endemism was reported by Lima (2000) and Sá (2006) who noted that most of the endemic species occurred in seasonal forests.

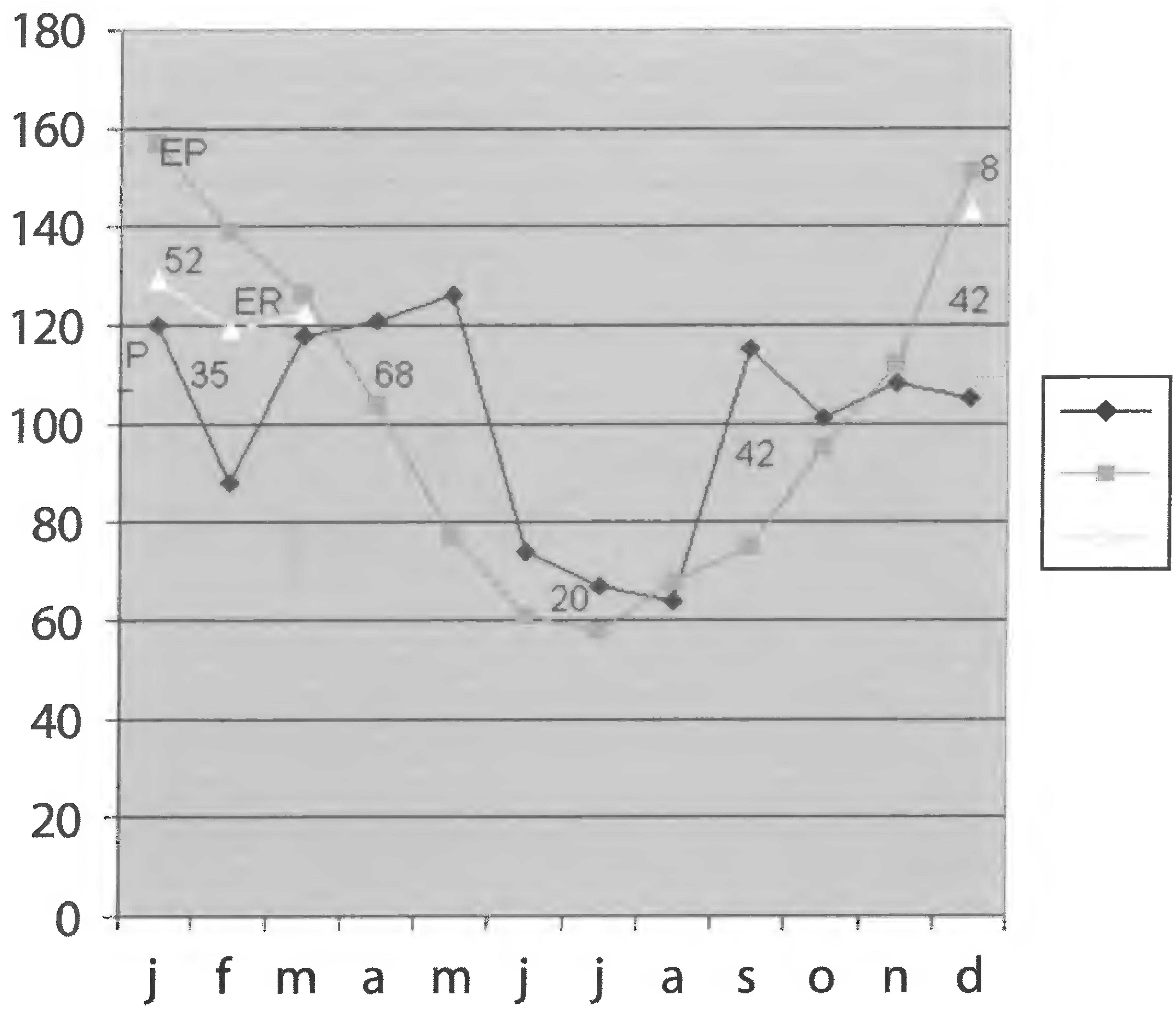

Fig. 3. Diagram of the water balance of Maricá (1987–99). Water Balance according to Thornthwaite & Mather (1955). Latitude: 22° 55'S - Longitude: 42° 49'W. Average Annual Temperature: 23.2° C. Annual Precipitation: 1207 mm = P. Annual Evapo-transpiration potential: 1223 mm = EP. True Annual Evapo-transpiration: 1163 mm = ER. Annual Water deficit: 60 mm. Annual Water Excess: 62 mm. Water Withdrawal: 81 mm; Water Replacement: 81 mm. Climatic type: Effective Humidity Index: sub-humid humid C2. Thermal efficiency: B´4 mesothermic.

The floristic diversity of the Morro Alto Mourão flora was high in comparison with these other areas of the Atlantic Coastal Forest (Horto/JBRJ and Morro das Andorinhas), even when allowing for the different methodologies and sample sizes used in the different surveys. The significant floristic diversity of this coastal mountainous region within the Serra do Mar Range is probably due to numerous factors, the most important likely being significant local climatic diversity (due to the unique geographic position of the Serra da Tiririca Range).

Physiognomic-floristic analysis

The vegetation on the Morro Alto Mourão is typical of the Serra do Mar Range. It can be classified as low-montane rain forest (Rizzini 1979). In regions where the eastern border of the Serra do Mar Range approach the coastline, the forest becomes smaller in stature (principally due to limiting edaphic conditions and slope) and acquires many elements of the near-shore (*restinga*) vegetation. There are also areas of shrubs/small trees and herbaceous vegetation near the rock outcrops. The different physiognomies observed on the Morro do Alto Mourão are illustrated in Figure 4.

In addition to the secondary forest formations in the study area (resulting from human intervention

Table 1. Numbers of families, genera, and specific and infra-specific taxa among the vascular flora in areas of Atlantic Coastal Forest within the state of Rio de Janeiro, Brazil.

	Alto Mourão	JBRJ/Horto1	Andorinhas2	Reserva Ecológica Macaé deCima3	APA-Cairuçu4	Reserva Biológica do Tinguá5
Families	84	74	60	122	133	124
Genera	244	168	103	413	483	421
Total taxa	369	277	105	1103	1087	1037

[1]Marquete et al. (1992); [2]Araujo and Vilaça (1981); [3]Lima and Guedes-Bruni (1997); [4]Marques (1997); [5]PMA/JBRJ (2002).

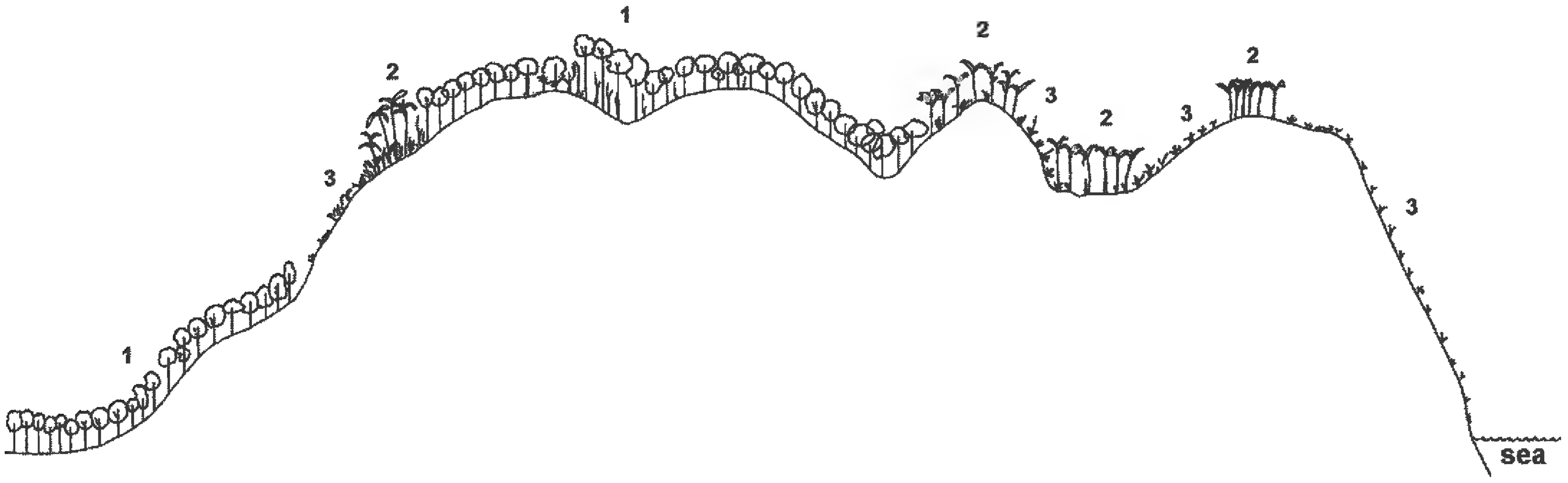

Fig. 4. Schematic profile of the phyto-physiognomies of the Morro Alto Mourão, Rio de Janeiro State, Brazil. 1. Arboreal formation; 2. Shrub-arboreal formation; 3. Herbaceous formation.

during the last three centuries) there are also small primary forest fragments. According to Pontes (1987), the Atlantic Coastal Forest once occupied the entire region around the Serra da Tiririca, but was subsequently subjected to extreme fragmentation through logging and clearing. Only isolated sections of the original forest remained in relatively inaccessible areas, such as Morro do Telégrafo and Morro Alto Mourão.

Edaphic and climatic factors must have played important roles in the establishment of plant communities or large populations in the area, resulting in the mosaic of successional stages found there today.

Despite the often imprecise limits of distinction between them, three principal physiognomic formations are recognized in this study: arboreal, shrub-arboreal, and herbaceous.

Arboreal formation

Arboreal formations dominate the study area and they presumably occupied an even greater proportion of the slopes in this region in earlier times. The topography is generally gentle and allows the accumulation of organic and inorganic material (the latter formed by the gradual breakdown of the rock substrate) that is necessary for soil formation and forest establishment. These arboreal formations now occupy the slopes and depressions, resulting in the formation of deep and fertile soils.

There are two forest layers—the upper and lower canopies, determined principally by the height of the component individuals (Fig. 5).

The upper canopy is closed and is composed of individuals that are generally between 12 and 25 m tall (remnants of the original forest). Some emergents are to be found, with average heights between 25 and 30 m, such as *Cariniana legalis*, *Anadenanthera colubrina*, *Pterogyne nitens*, *Schinus terebenthifolius*, *Gallesia integrifolia* and *Coussapoa curranii*.

The lower canopy is composed of individuals that are between 5 and 12 m tall. This layer is more open, and the tree crowns being more widely spaced. Some representative species are: *Piptadenia gonoacantha*,

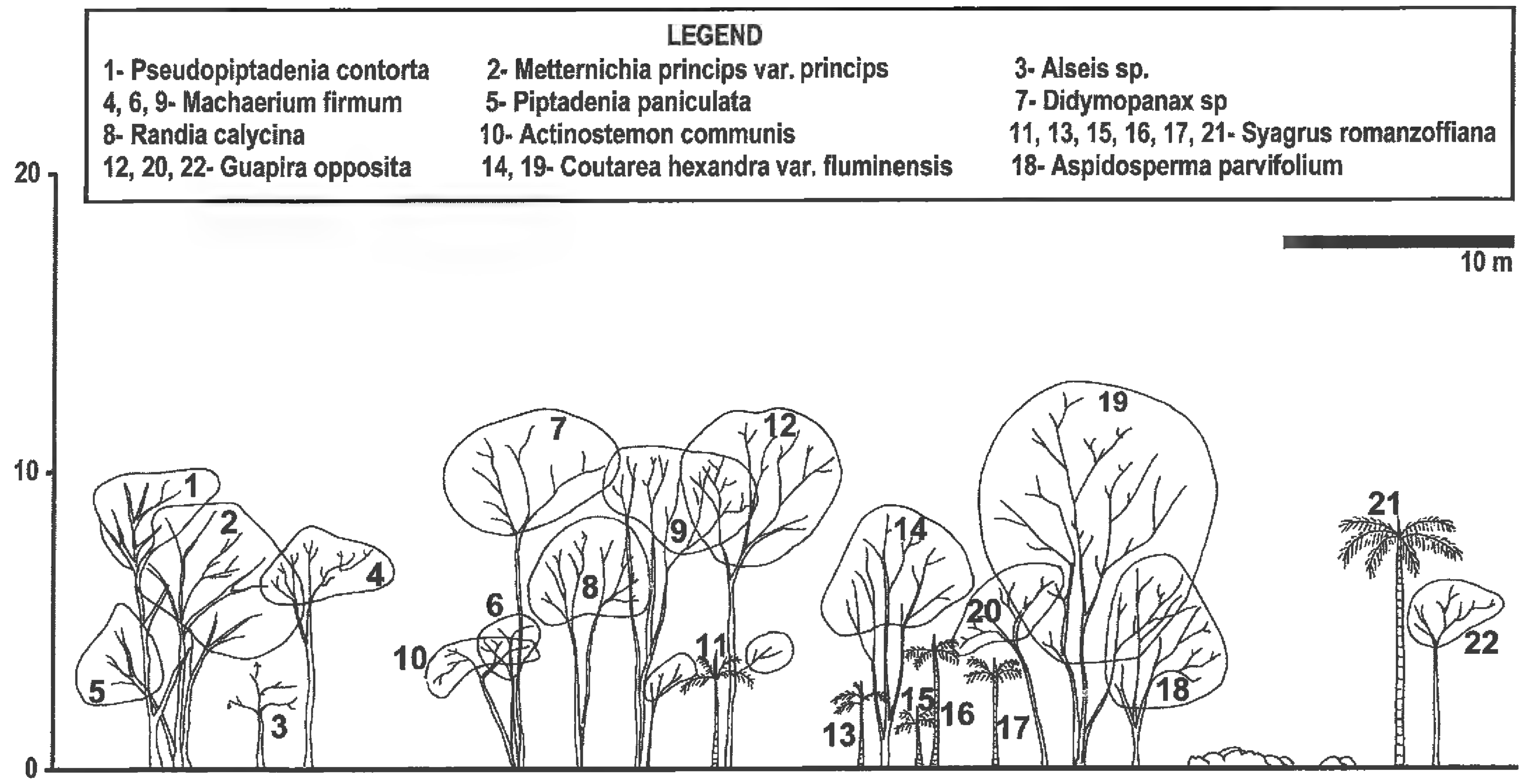

Fig. 5. Schematic profile of the arboreal formation of the Morro Alto Mourão, Rio de Janeiro State, Brazil.

Erythroxylum pulchrum, *E. frangulifolium*, *Metternichia principis* var *principis*, *Pseudobombax grandiflorum*, *Guapira opposita*, and *Casearia sylvestris* var. *sylvestris*.

The shrub-arboreal formation

A shrub-arboreal vegetation predominates on the ocean-facing mountain slopes. This vegetation is very dense, with a xeromorphic aspect. However, it has a small number of emergent species (Fig. 6). Species common to the sandy near-shore (*restinga*) vegetation, such as *Clusia fluminensis* and *Brasiliopuntia brasiliensis* are also present.

This formation has reasonably large populations of plants that stand out physiognomically in the vegetation, such as *Marlierea racemosa*, *Eugenia uniflora*, *Myrcia insularis*, *M. richardiana*, and *Psidium cattleyanum* (all of the Myrtaceae family) that vary in height from 5–7 m. *Pachystroma longifolium* can reach up to 10 m. There are also smaller populations of *Esenbeckia febrifuga* growing together with the palm tree *Syagrus romanzoffiana* (that can reach 10–15 m).

Clavija spinosa, *Jacaranda jasminoides*, *Inga congesta*, *Brunfelsia uniflora*, *Norantea brasiliensis*, *Cupania racemosa*, *Tibouchina corymbosa*, and *Faramea stipulacea* are well represented among the shrubs.

This same shrub-arboreal vegetation harbors numerous herbaceous and sub-shrub species (e.g., *Justicia beyrichii*, *Sinningia aggregata*, *Eupatorium organense*, *Julocroton triqueter*, *Capparidastrum brasilianum*, *Cyperus diffusus*, *Calathea truncata*, *Selaginella sulcata*, *Alstroemeria caryophyllea*, and *Neomarica* sp.). These cannot be considered a distinct formation in themselves as they are very thinly distributed within the area. On the other hand, there are dense populations of *Schaueria calycotricha* in shaded areas at the forest edge, near rock outcrops with many weedy plants such as *Petiveria alliacea*, *Sida rhombifolia*, *Oxalis barrelieri*, *Solanum alternopinnatum*, and *Stachytarpheta polyura*, as well as epiphytes and vines.

Epiphytes and hemi-epiphytes are relatively uncommon in the area. They include *Anthurium pentaphyllum*, *A. scandens* subsp. *scandens*, *Monstera adansonii* var. *klotzschiana*, *Philodendron bipennifolium*, *P. cordatum*, *Aechmea nudicaulis* var. *nudicaulis*, *Neoregelia ampullacea*, *Billbergia pyramidalis* var. *pyramidalis*, *Rhipsalis teres* f. *capilliformis*, *R. mesembryanthemoides*, *R. neves-armondii*, and *R. pachyptera*, among other taxa of Gesneriaceae, Orchidaceae, Piperaceae, and Pteridophytes.

Some epiphytes are encountered in the area with other life forms, such as *Anthurium scandens* subsp.

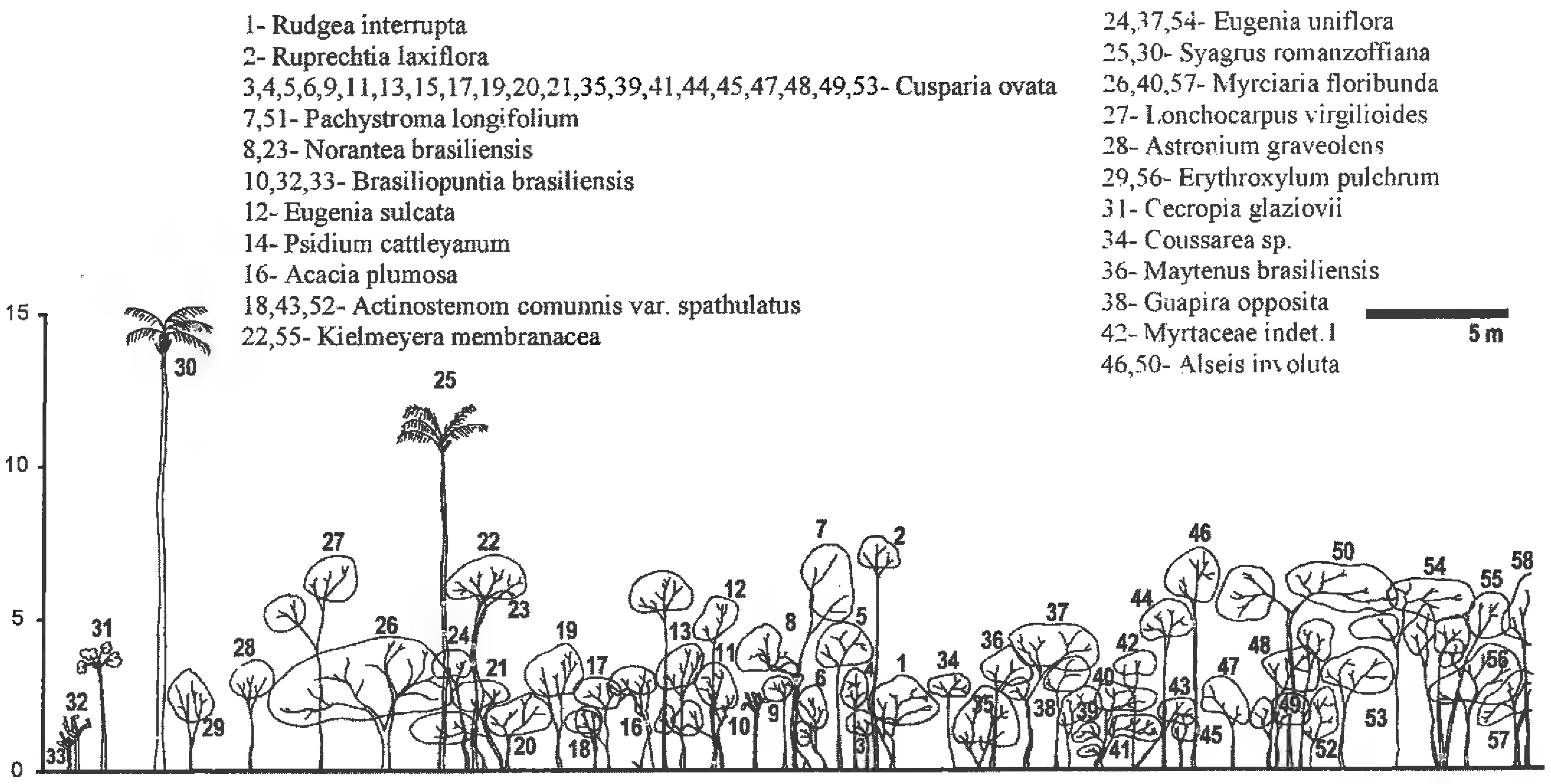

Fig. 6. Schematic profile of the shrub-arboreal formation of the Morro Alto Mourão, Rio de Janeiro State, Brazil.

scandens, as rupicolous, and terrestrial individuals of *Philodendron cordatum*. Also *Oncidium* and *Pleurothallis* species are encountered both as epiphitic and rupicolous.

Both woody and non-woody vines are found on the Morro Alto Mourão, especially species belonging to the genera *Adenocalymma*, *Anemopaegma*, *Bauhinia*, *Chaetocalyx*, Centrosema, *Serjania*, *Paullinia*, *Urvillea*, *Heteropterys*, *Tetrapterys*, *Chondrodendron*, *Hyperbaena*, *Passiflora*, *Ipomoea*, *Jacquemontia*, *Reissekia*, *Dioscorea*, *Smilax*, and *Herreria*.

A single species of the hemi-parasite *Struthanthus marginatus* was encountered.

The herbaceous formation

This vegetation type is typically found on rock outcrops where plants grow directly on the rock surface (rupicolous) or within thin sandy strips of soil near the rock outcrops (saxicolous). The plants at these sites are exposed to extreme environmental conditions due to their proximity to the ocean, including high levels of solar radiation, strong, constant winds and high salinity (Fig. 7).

Tillandsia dura, *Aechmea ramosa* var. *ramosa*, *Neoregelia ampullacea*, *Peperomia incana*, *P. corcovadensis*, *Cyrtopodium polyphyllum*, *Anthurium coriaceum*, *A. olfersianum*, *Philodendron speciosum*, *Coleocephalocereus fluminensis*, *Rhipsalis cereoides*, and *Hylocereus setaceus* are among the most frequent Angiosperm pioneer species.

There are also small clumps of plants found in deeper soils areas, including individuals of *Tibouchina corymbosa*, *Tabebuia chrysotricha*, and *Stillingia dichotoma*, in addition to the pioneer species.

Other communities are found on flat rocky surfaces in natural clearings within the forest (240–260 m altitude) on very humid soils and include *Sebastiania brasiliensis*, *Cnidoscolus urens*, *Furcraea gigantea*, *Galactia striata*, and *Stylosanthes scabra*, as well as plants considered invader species, such as *Cleome dendroides* subsp. *dendroides*, *Manihot palmata*, *Dichorisandra thyrsiflora*, and *Tradescantia zebrina*.

Conservation

This area is significant because it contains a large number of species (20) endemic to the State of Rio de Janeiro, some of which are limited to the the Serra do Mar forests (Appendix 1). Among the most interesting of these are *Picramnia grandifolia* and *Philodendron speciosum*, both of which were considered practically extinct and are known from only two previous collections in Atlantic Coastal Forest areas (Pirani 1990; Mayo 1991). *Wilbrandia glaziovii* (Cucurbitaceae) had not been found growing in the wild since the 19th century

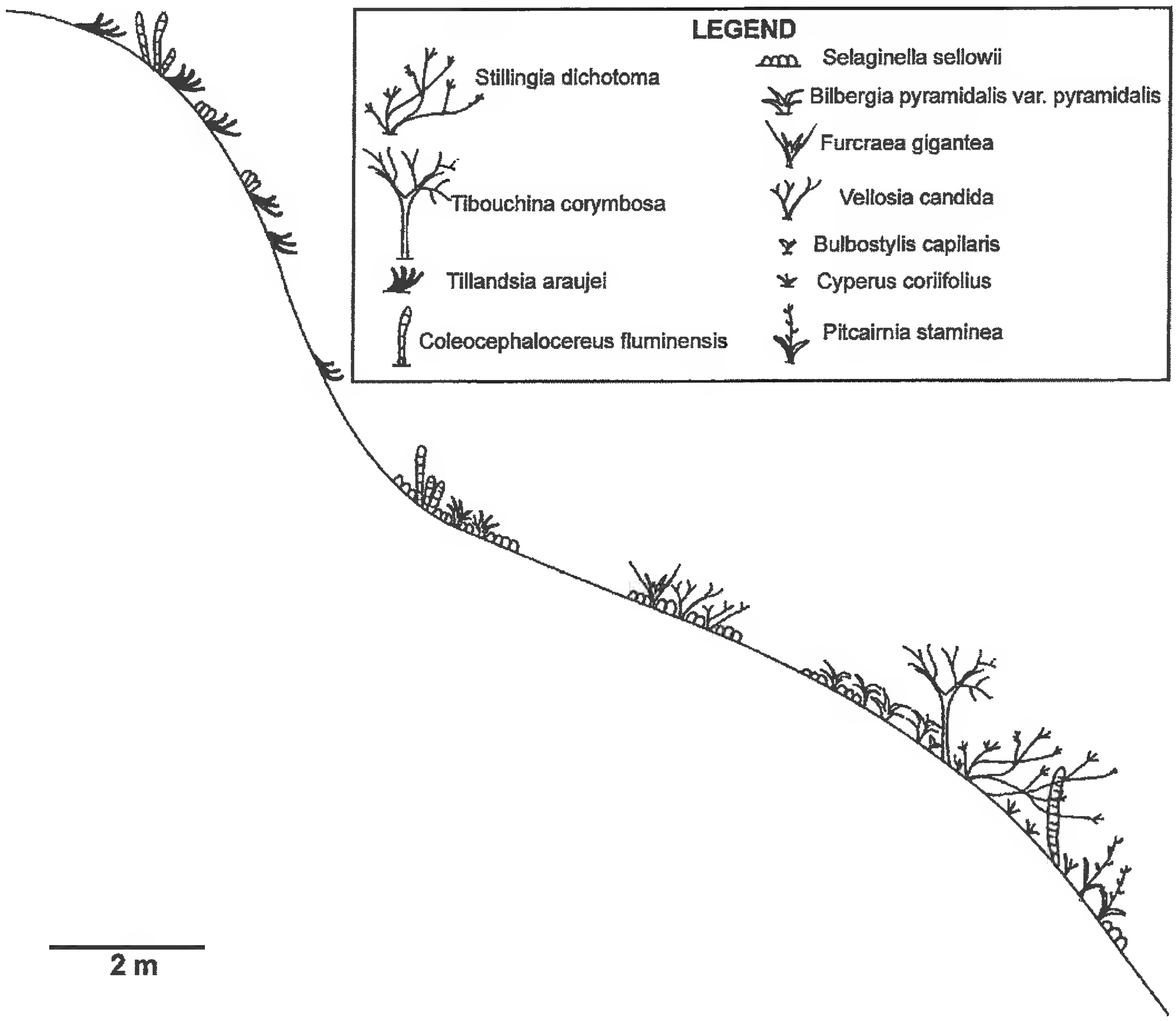

Fig. 7. Schematic profile of the herbaceous formation of the Morro Alto Mourão, Rio de Janeiro State, Brazil.

(Klein 1990). Also relevant is the finding of species that are considered either rare and/or threatened, such as *Pterogyne nitens*, *Pouteria subsessilifolia* (IUCN 2004) and *Astronium glaziovii*. The latter species has only a few collections registered in all of the Brazilian herbaria (Santin 1989). Among the plants encountered that are threatened with extinction in the municipality of Rio de Janeiro are *Inga congesta*, *Inga cordistipula*, and *Lonchocarpus virgilioides* (Lima 2000a). Additionally, *Ficus enormis* and *Coleocephalocereus fluminensis* are considered to be threatened due to destruction of their habitat in the State of Rio de Janeiro (Duarte et al. 2003; Calvente et al. 2005). Other rare species are *Gomidesia sonderiana*, which has rarely been found in the Atlantic Coastal Forest (Nic Lughadha, pers. comm.); *Alstroemeria caryophyllaea*, which had only previously been encountered growing in the wild humid and shady areas in the States of Minas Gerais and Rio de Janeiro (Assis 2004); *Pleurothallis pardipes*, recollected recently in Parque Municipal da Prainha, Rio de Janeiro State (Pinheiro 1999).

The occurrence of these rare and/or threatened species, together with numerous cases of endemism, illustrates the importance of conserving the Morro Alto Mourão area. These (and other) species could potentially be utilized as germplasm sources for seedlings production used to replant other fragments with a similar floristic compositions in the Rio de Janeiro Atlantic Coastal Forest.

It is important to note that the Morro Alto Mourão area contains a considerable number of species useful

to humans or with significant direct economic potential (see Lopes 1992), including those with medicinal (Lopes & Andreata 1989, 1990, 1991, 1992) and ornamental (Lopes et al. 2004) uses.

The economic potential of these plants, together with the proximity of the Morro Alto Mourão area to a large urban centre, complicates its preservation. Barros and Seone (1999) have proposed strategies for the conservation of areas within the Serra da Tiririca State Park including monitoring to combat plant resources extraction and fires, as well as controlling tourism.

CONCLUSIONS

The best represented plant families observed in the Morro Alto Mourão area followed the same patterns seen in other floristic inventories undertaken in the State of Rio de Janeiro (Marquete et al. 1992; Araujo & Vilaça 1981; Lima & Guedes-Bruni 1997; Marques 1997; PMA/JBRJ 2002).

The phyto-physiognomic analysis of this area revealed a significant vegetation cover (predominantly arboreal) in spite of both the historical and recent environmental aggression.

The eastern portion of the Guanabara Bay in the municipality of Niterói has only a few small forest fragments remaining, including the Serra da Tiririca (FEEMA 1977). This fact and the other data presented in this work reinforce the fundamental importance of preserving the biodiversity present within the Atlantic Coastal Forest in the State of Rio de Janeiro.

APPENDIX 1

List of the vascular plants of the Morro Alto Mourão, Rio de Janeiro State, Brazil by alphabetical order of the families, citing the specialists consulted, Latin name, habit, flowering (fl), fruiting (fr), and collector's name (*endemic), (**introduced).

PTERIDOPHYTES (P. Windisch & C. Mynssen)

Pteridaceae

Doryopteris collina (Raddi) J. Sm. – herb, R. Andreata 330
Doryopteris lomariacaea Klotzsch – herb, R. Andreata 898
Doryopteris patula (Fée) Fée – herb, V. Ferreira 2107
Doryopteris varians (Raddi) J. Sm. – herb, R. Andreata 34, 530

Schizaeaceae

Anemia phyllitidis Sw. – herb, R. Andreata 35, 443

Selaginellaceae

Selaginella sulcata (Desv. ex Poir.) Spring ex Mart. – herb, V. Ferreira 2106
Selaginella sellowii Hieron. – herb, R. Andreata 51, 879

DICOTYLEDONS

Acanthaceae

Aphelandra longiflora (Lindl.) Profice – shrub, fl (Nov), fr (Nov), R. Andreata 602
Chamaeranthemum beyrichii Nees – herb, fl (Apr), R. Andreata 426
Justicia beyrichii Nees – herb, fl (May, Sep, Nov), R. Andreata 520, 523, 560, 607
Justicia sp. – sub-shrub, fl (Apr–May), R. Andreata 415, S. Profice 577
Ruellia solitaria Vell. – herb, fl (Aug), R. Andreata 92
**Schaueria calycotricha* (Link. & Otto) Nees – shrub, fl (Jul, Oct–Dec), fr (Jul–Sep, Oct–Nov), R. Andreata 47, 91, 131, 335, 479
Thunbergia alata Bojer ex Sims. – climbing, fl (Nov), fr (Jul), R. Andreata 24, 453

Amaranthaceae

Alternanthera sp. – herb, fl (Jan), R. Andreata 405
Alternanthera brasiliana (L.) Kuntze var. *villosa* (Moq.) Kuntze – herb, fl (May–Jul), R. Andreata 72, 704

Anacardiaceae (F. Gil)

Astronium glaziovii Mattick – tree, fl (sterile), R. Andreata 359, 361, 716, 719
Astronium graveolens Jacq. – tree, fl (Jul), R. Andreata 85, 360, 369, 719, 721, 969
Schinus terebinthifolius Raddi – tree, R. Andreata 349
Spondias mombin L. – tree, fl (Sep), fr (Jan), R. Andreata 357, 504, 915
Spondias venulosa Mart. ex Engl. – tree, R. Andreata 915; G.Lewis 3988; D.Santin s.n.

Annonaceae (C.G.P. Quinet)

Rolliniopsis parviflora (A. St.-Hil.) Saff., small tree, fl (Nov), fr (Jan), R. Andreata 403, 615; C. Farney 363

Apocynaceae

Aspidosperma sp. – tree, fl (Jan), V. Ferreira 2094
Aspidosperma parvifolium A.DC. – tree, fl (sterile), R. Andreata 696
Aspidosperma tomentosum Mart. – tree, fl (Sep), fr (Sep), R. Andreata 922
Mandevilla funiformis (Vell.) K. Schum. – climbing, fl (Jul), fr (Jul), R. Andreata 476
Tabernaemontana sp. – tree, fl (Nov), R. Andreata 609
Tabernaemontana hystrix Steud. – tree, fl (Nov–Dec), R. Andreata 60; C. Farney 368
Prestonia cf. *calycina* Müll. Arg. – climbing, sterile, R. Andreata 118a

Prestonia coalita (Vell.) Woodson – climbing, R. Andreata 705

Araliaceae

Schefflera succinea Frodin & Fraschi – tree, fl (sterile), R. Andreata 682

Aristolochiaceae

Aristolochia rumicifolia Mart. & Zucc. – climbing, fl (Sep), R. Andreata 525

Howardia cymbifera (Mart. & Zucc.) Klotzsch – climbing, fl (sterile), R. Andreata 487

**Howardia raja* (Mart. & Zucc.) Klotzsch – climbing, fl (Oct–Dec), fr (Sep), R. Andreata 37, 147, 193, 513

Asclepiadaceae (N. Marquete F. Silva)

Oxypetalum banksii Roem. & Schult. subsp. *banksii* – climbing, fl (Jul, Sep), R. Andreata 96, 544

Asteraceae (R. Esteves)

Centratherum punctatum Cass. var. *punctatum* – herb, fl (Dec), R. Andreata 19

Cyrtocymura scorpioides (Lam.) H. Rob. – sub-shrub, fl (Apr, Aug, Dec), R. Andreata 33, 87, 674

Eupatorium organense Gardner – sub-shrub, fl (Nov–Dec), R. Andreata 57, 314

Eupatorium vitalbae DC. – herb, fl (Aug), R. Andreata 105

Gochnatia sp. – tree, fl (Jan), R. Andreata 364

Tilesia baccata (L.) Pruski – shrub, fl (Oct), fr (Oct), R. Andreata 123, 127

Begoniaceae

Begonia sp. – herb, fl (Nov–Dec), R. Andreata 46, 194

Bignoniaceae

Adenocalymma paulistarum Bureau – climbing, fl (Jan, Dec), R. Andreata 48, 354

Anemopaegma chamberlaynii (Sim) Bureau & K. Schum – climbing, fr (May), R. Andreata 552

Arrabidaea aff. rego (Vell.) DC. – tree, fl (Apr), fr (Apr), R. Andreata 669

Cybistax antisyphilitica (Mart.) Mart. – tree, fl (May, Nov), fr (Jan), R. Andreata 318, 347, 666

Jacaranda jasminoides (Thunb.) Sandwith – shrub, fl (Aug, Oct–Dec), fr (Jul, Oct–Nov), R. Andreata 55, 89, 122, 165, 301, 316, 323

Pithecoctenium crucigerum (L.) A.H. Gentry – climbing, fr (May), R. Andreata163; C. Farney 740

Sparattosperma vernicosum Bureau & K. Schum. – tree, fl (sterile), R. Andreata 372

Tabebuia sp. – tree, fl (sterile), R. Andreata 988

Tabebuia chrysotricha (Mart. ex DC.) Standl. – tree, fl (Aug), fr (Aug), R. Andreata 104

Bombacaceae

Bombacopsis glabra (Pasq.) A. Robyns – tree, fl (Sep), fr (Jan–Feb, Apr), R. Andreata 346, 496, 665; T. Plowman 12858

Ceiba insignis (Kunth) P.E. Gibbs & Semir – tree, fl (Apr), R. Andreata 376, 897

Pseudobombax grandiflorum (Cav.) A. Robyns – tree, fl (Jul), R. Andreata 455, 713, 985

Quararibea turbinata (Sw.) Poir. – shrub, fr (May, Jul), R. Andreata 461, 581

Boraginaceae

Cordia ochnacea DC. – shrub, fl (Nov), fr (Apr–May), R. Andreata 344, 587, 589, 610, 667

Cordia trichotoma (Vell.) Arrab. ex Steud. – tree, fl (Apr–May), R. Andreata 549, 663, 910, 912

**Tournefortia salicifolia* A. DC. – sub-shrub, fl (Sep, Nov), R. Andreata 334, 546

Cactaceae (L. Scheinvar and A.M. Calvente)

Brasiliopuntia brasiliensis (Willd.) A. Berger – tree, fl (Oct), fr (Oct), R. Andreata 130

Coleocephalocereus fluminensis (Miq.) Backeb. – herb, fl (Apr), R. Andreata 889

Hylocereus setaceus (Salm-Dyck ex DC.) Ralf Bauer – epiphytic, fl (Nov), R. Andreata 304

Rhipsalis cereoides (Backeb. & Voll.) Backeb. – epiphytic, fl (Apr), fr (Sep), R. Andreata 326, 545, 650, 886; T. Plowman 13935

Rhipsalis dissimilis K. Schum. – epiphytic, V. Ferreira 2115

**Rhipsalis mesembryanthemoides* Haw. – epiphytic, fl (Nov), R. Andreata 301; G. Martinelli 8154

Rhipsalis neves-armondii K. Schum. – epiphytic, fl (May), fr (May), R. Andreata 303, 592

Rhipsalis pachyptera Pfeiff. – epiphytic, fl (sterile), R. Andreata 302

Rhipsalis teres Steud. f. *capilliformis* (F.A.C. Weber) Barthlott & Taylor – epiphytic, fl (sterile), R. Andreata 327

Capparaceae

Capparidastrum brasilianum (DC.) Hutch. – sub-shrub, fl (Nov), fr (Jul), R. Andreata 467, 611, 950

Cleome dendroides Schult. subsp. dendroides – shrub, R. Andreata 42, 106, 185

Celastraceae (A. Joffily)

Maytenus brasiliensis Mart. – shrub, fl (Apr), fr (Nov), R. Andreata 425, 973

Maytenus communis Reissek – shrub, fr (Aug), R. Andreata 482

Clusiaceae

Clusia fluminensis Planch. & Triana – tree, fl (Nov), R. Andreata 306

Garcinia gardneriana (Planch. & Triana) Zappi – shrub, fl (Nov), R. Andreata 202

Kielmeyera membranacea Casar. – tree, fl (Jan–Feb), fr (Jan–Feb, Jun–Jul), R. Andreata 370, 456, 714,725; T. Plowman 13929

Convolvulaceae

Argyreia baronii Deroin – climbing, fl (Sep), R. Andreata 538

Ipomoea grandifolia (Dammer) O'Donell – climbing, fl (Jan), fr (Jan), R. Andreata 367

Jacquemontia martii Choisy – climbing, fl (Apr, Dec), R. Andreata 411

Cucurbitaceae (V.L.G. Klein)

**Wilbrandia glaziovii* Cogn. – climbing, fl (Oct), fr (Sep), R. Andreata 129, 924

Elaeocarpaceae

Sloanea garckeana K. Schum. – tree, fl (Jan), fr (Jan), R. Andreata 382

Erythroxylaceae (T. Plowman)

Erythroxylum frangulifolium A. St.-Hil. – tree, fl (Feb, Jul, Aug–Sep, Nov), fr (Feb, Jul, Sep–Nov), R. Andreata 70, 169, 501, 641; C. Farney 362; T. Plowman 12860, 13922, 13926; V.Fereira 2239

Erythroxylum gaudichaudii Peyr. – shrub, fl (Jan–Feb), fr (Jan–Feb), R. Andreata 400; T. Plowman 13929, 13930

Erythroxylum pulchrum A. St.-Hil. – tree, fl (sterile), R. Andreata 350, 375, 970, 984

Euphorbiaceae (L.S. Vale and A. Sousa)

Acalypha brasiliensis Mül. Arg. var *brasiliensis* – sub-shrub, fl (Aug, Dec), R. Andreata 21, 73, 919, 979

Actinostemon communis (Müll. Arg.) Pax var. *spathulatus* Mül. Arg. – shrub, fl (Aug), fr (Aug–Sep), R. Andreata 77, 79, 686, 689, 966, 979, 982

Actinostemon concolor (Spreng.) Müll. Arg. var. obovatus Mül. Arg. – shrub, fl (Aug, Oct–Nov), fr (Jul, Sep–Nov), R. Andreata 162, 300, 536, 618

Cnidoscolus urens (L.) Arthur – herb, fl (Dec), R. Andreata 43

Croton compressus Lam. – shrub, fl (Dec–Jan), R. Andreata 56, 378

Croton klotzschii (Diedr.) Müll. Arg. – sub-shrub, fl (Dec), R. Andreata 58

Croton urticifolius Lam. – sub-shrub, fl (Dec), R. Andreata 26

Dalechampia alata Müll. Arg. – climbing, fl (Dec–Jan), R. Andreata 61, 362

Dalechampia micromeria Bail. – climbing, fl (Nov), fr (Nov), R. Andreata 333

Euphorbia comosa Vell. – sub-shrub, fl (Oct, Dec), fr (Oct), R. Andreata 37, 182

Julocroton triqueter (Baill.) Müll. Arg. – sub-shrub, fl (Dec), fr (Jan), R. Andreata 22

Joannesia princeps Vell. – tree, fl (sterile), R. Andreata 992

Manihot inflata Müll. Arg. – shrub, fl (Jan), fr (Jan), V. Ferreira 2095

Manihot palmata (Vell.) Müll. Arg. – shrub, fl (Jan, Dec), R. Andreata 44, 368

Manihot tripartita (Spreng.) Müll. Arg. subsp. *humilis* (Müll. Arg.) Roger – shrub, fl (Nov), fr (Nov), R. Andreata 614

Pachystroma longifolium (Nees) I.M.Johnst. – tree, fl (Feb, Nov), fr (Feb, Aug), R. Andreata 463, 957; T. Plowman 13927

Phyllanthus subemarginatus Müll. Arg. – sub-shrub, fl (Sep), fr (Sep), R. Andreata 541

Plukenetia serrata (Vell.) L.J. Gillespie – climbing, v.v.

Romanoa tamnoides (A. Juss.) Radcl.-Sm. – climbing, fl (Apr), fr (Apr), Andreata 883

Sapium glandulosum (L.) Morong – tree, fl (sterile), R. Andreata 380

Sebastiania brasiliensis Spreng. – shrub, fr (Apr), R. Andreata 132, 178

Stillingia dichotoma Müll. Arg. – shrub, fl (Apr, Nov), fr (Apr), R. Andreata 339, 675, 885

Tragia volubilis L. – climbing, fl (Jan), V. Ferreira 2117

Flacourtiaceae (R. Marquete)

Casearia leutzelburgii Sleumer – tree, fr (Aug), R. Andreata 94, 722, 727

Casearia obliqua Spreng. – tree, fl (sterile), R. Andreata 914

Casearia sylvestris Sw. var. *sylvestris* – tree, fl (Aug–Sep), fr (Sep), R. Andreata 909, 925, 991; V. Ferreira 2238

Gesneriaceae (A. Chautems and T.C.C. Lopes)

Codonanthe gracilis (Mart.) Hanst. – herb, fl (Nov), R. Andreata 340

Paliavana prasinata (Ker Gawl.) Benth. – sub-shrub, fl (May, Jul), fr (Aug), R. Andreata 90, 584; C. Farney 736

Sinningia aggregata (Ker Gawl.) Wiehler – herb, fl (Sep), fr (Sep), R. Andreata 62, 542; G. Martinelli 8520

Lauraceae (A. Quinet)

Aniba brittonii Mez. – tree, fr (Apr, Jul), R. Andreata 442, 489; V. Ferreira 2121

Ocotea aniboides Mez – shrub, fr (Nov), R. Andreata 941

Ocotea brachybotra (Meisn.) Mez – tree, fr (Nov), R. Andreata 943

Phyllostemonodaphne geminiflora (Mez) Kosterm. – shrub, fl (Jan), R. Andreata 389, 446

Lecythidaceae

Cariniana legalis (Mart.) Kuntze – tree, fl (sterile), R. Andreata 381

Leguminosae (Caesalpinioideae)

Bauhinia radiata Vell. – climbing, fl (sterile), R. Andreata 196

Bauhinia microstachya (Raddi) J.F. Macbr. – climbing, fl (sterile), R. Andreata 164, 575

Chameacrista fasciculata (Michx.) Greene – sub-shrub, fl (Dec), R. Andreata 28, 112

Chamaecrista glandulosa (L.) Greene var. *brasiliensis* (L.) H.S. Irwin & Barneby – sub-shrub, fl (Nov), fr (Apr, Nov), R. Andreata 651, 670; H.C. Lima 2069

Copaifera trapezifolia Hayne – tree, R. Andreata 164, 576

Pterogyne nitens Tul. – tree, fl (Apr), fr (Apr), R. Andreata 394, 662, 911

Senna affinis (Benth.) H.S. Irwin & Barneby – shrub, fr (Apr), R. Andreata 410

Senna macranthera (DC. ex Colladon) H.S. Irwin & Barneby – tree, fl (May), fr (May), C. Farney 729

Senna tenuifolia (Vogel) H.S. Irwin & Barneby – shrub, fl (Apr), R. Andreata 410; H.C. Lima 3714

Leguminosae (Papilionoideae)

Acosmium lentiscifolium Schott ex Spreng. – shrub, fl (sterile), R. Andreata 931; H.C. Lima 3734

Centrosema sagittatum (Willd.) Ridley – climbing, fl (May), fr (May), H.C. Lima 2592, 2600

Chaetocalyx scandens (L.) var. *pubescens* (DC.) Rudd – climbing, fl (Oct–Dec), fr (Oct, Dec), R. Andreata 36, 128, 175

Dalbergia frutescens (Vell.) Britt., small tree, H.C. Lima 3715

Desmodium affine Schltdl. – herb, fl (Apr), R. Andreata 447

Desmodium incanum (Sw.) DC. – herb, fl (Dec), fr (Dec), R. Andreata 25

Galactia striata (Jacq.) Urb. – herb, fl (Jan), fr (Jan), R. Andreata 366

Lonchocarpus virgilioides (Vogel) Benth. – tree, fl (Sep), fr (Sep), R. Andreata 141, 529, 724, 726, 904, 916
Machaerium firmum (Vell.) Benth. – tree, fl (sterile), R. Andreata 371, 679, 681, 685
Machaerium hirtum (Vell.) C. Stellfeld – tree, fl (sterile), R. Andreata 893
Machaerium oblongifolium Vogel – climbing, fl (sterile), R. Andreata 891
Machaerium pedicellatum Vogel, small tree, fl (sterile), R. Andreata 892, 930
Machaerium violaceum Vogel – climbing, fl (sterile), R. Andreata 899; H.C. Lima 2596
Pterocarpus rohri Vahl – tree, fl (sterile), R. Andreata 895
Stylosanthes scabra Vogel – herb, fl (Oct), R. Andreata 135
Vigna sp. – sub-shrub, fl (May), C. Farney 733
Zornia latifolia Sm. – sub-shrub, fl (sterile), R. Andreata 887

Leguminosae (Mimosoideae)
Acacia plumosa Lowe – shrub, fl (Nov), fr (Feb, Apr, Nov), R. Andreata 600, 884, 964; H.C. Lima 3732
Acacia mikanii Benth. – shrub, fl (Nov), R. Andreata 575, 616
Albizia polycephala (Benth.) Killip – tree, fl (Jan), fr (Jan, May), R. Andreata 363, 550
Anadenanthera colubrina (Vell.) Brenan – tree, fr (Jan), R. Andreata 348
Inga bullata Benth. – tree, I.A.Rodrigues s.n.
Inga congesta T.D. Penn. – shrub, fl (Jul–Aug), fr (Jul–Oct), H.C. Lima 2603[A], 3991; R. Andreata 87, 125, 449, 451, 509
Inga cordistipula Mart. – tree, fl (Jan–Feb), fr (May), R. Andreata 397, 583, 639, 1003
Mimosa arenosa (Willd.) Poir. – sub-shrub, fl (Apr), R. Andreata 900
Mimosa bimucronata (DC.) Kuntze – shrub, fl (Apr), fr (Apr,Jun), R. Andreata 409, 452, 902
Mimosa extensa Benth. – climbing, fl (Nov), H.C. Lima 3733
Mimosa velloziana Mart. – shrub, fl (Apr), fr (Apr, Jul), R. Andreata 485, 660
Piptadenia gonoacantha (Mart.) J.F. Macbr. – tree, fl (Feb), fr (May), R. Andreata 586; H.C. Lima 3738
Piptadenia paniculata Benth. – tree, fl (Feb), fr (May), R. Andreata 353, 393, 547, 680; H.C. Lima 3714
Pseudopiptadenia contorta (DC.) G.P. Lewis & M.P.M. Lima – tree, fr (May), R. Andreata 585, 676

Loganiaceae
Strychnos acuta Progel – sub-shrub, fl (Sep), fr (Apr), R. Andreata 421, 944
Strychnos trinervis (Vell.) Mart. – shrub, fr (Jan), R. Andreata 383

Loranthaceae
Struthanthus marginatus (Desr.) Blume, hemi-parasite, fl (Oct), fr (Oct), R. Andreata 115, 117

Lythraceae
Cuphea carthagenensis (Jacq.) J.F. Macbr. – herb, fl (Dec), R. Andreata 39

Malphighiaceae (W.R. Anderson and A. Amorim)
Amorimia rigida (A. Juss.) W.R. Anderson – climbing, fl (Jan), fr (Jun), R. Andreata 373, 708
***Bunchosia glandulifera* (Jacq.) H.B.&K. – shrub, fr (Apr), R. Andreata 664
Bunchosia maritima (Vell.) J.F. Macbr. – shrub, fl (Oct–Dec), fr (May), R. Andreata 41, 111, 166, 558, 890
Heteropterys bicolor A. Juss. – climbing, fr (Jan), V. Ferreira 2100; R. Andreata 101, 528
Heteropterys pauciflora (A. Juss.) A. Juss. – shrub, fl (Sep), fr (Jul), R. Andreata 488
Heteropterys sericea (Cav.) A. Juss. – climbing, fl (Jan), R. Andreata 390
**Heteropterys ternstroemiifolia* A. Juss. – climbing, fr (Jul), R. Andreata 475
Niedenzuella acutifolia (Cav.) W.R. Anderson – shrub, climbing, fl (Aug–Dec), fr (Jan, Aug), R. Andreata 152,155, 322, 345, 510, 636

Malvaceae (M.G. Bovini)
Abutilon bedfordianum (Hook.) A. St.-Hil. & Naudin – shrub, fr (May), R. Andreata 524, 590
Pavonia sepium A. St.-Hil. – sub-shrub, fl (Apr), fr (Apr), R. Andreata 431
Sida rhombifolia L. – sub-shrub, fl (Dec), R. Andreata 15

Marcgraviaceae
Norantea brasiliensis Choisy – shrub, fl (Nov), fr (Jan), R. Andreata 309, 401, 986

Melastomataceae
Clidemia hirta (L.) D. Don – shrub, fl (Nov), fr (Jul, Sep), R. Andreata 188, 492
Miconia cinerascens Miq. – shrub, fl (Apr–May, Sep, Nov), fr (May, Sep, Nov), R. Andreata 138, 184, 414, 493, 933; C. Farney 730
Miconia staminea (Desr.) DC. – shrub, fl (Nov), fr (Nov), R. Andreata 186
Ossaea marginata (Desr.) Triana – shrub, fl (Sep–Nov), R. Andreata 144, 187, 515
Tibouchina corymbosa (Raddi) Cogn. – shrub, fl (Nov–Jan), R. Andreata 59, 317, 377, 901

Meliaceae
Guarea guidonia (L.) Sleumer, fl (Nov), R. Andreata 189; V. Ferreira 2093
Trichilia alternans DC. – tree, fl (Oct–Nov), R. Andreata 143, 170
Trichilia casaretii DC. – tree, fr (Apr, Jul), R. Andreata 423, 450
Trichilia elegans A. Juss. subsp. *richardiana* Penn. – shrub, fl (Nov), fr (Jul), R. Andreata 308, 482
Trichilia pseudostipularis (A. Juss.) DC. – shrub, fl (Jan, Nov), fr (May), R. Andreata 402, 594
Trichilia silvatica DC. – shrub, fl (Nov), fr (Aug), R. Andreata 107, 935

Menispermaceae (J.M.A. Braga)
Chondrodendron platyphyllum (A. St.-Hil.) Miers – climbing, fr (Apr), R. Andreata 419
**Hyperbaena oblongifolia* (Mart.) Chodat – climbing, fl (Jul, Sep), fr (Sep), R. Andreata 502; V. Ferreira 2235

Moraceae (J.P.P. Carauta)
Cecropia glaziovii Snethl. – tree, fl (sterile), R. Andreata 937, 971

Coussapoa curranii J.M. Blake – tree, fl (Jul), R. Andreata 457
Dorstenia arifolia Lam. – herb, fl (Jan, Nov), R. Andreata 183, 395, 646; V. Ferreira 2124
Dorstenia cayapia Vell. – herb, V. Ferreira 2102
Dorstenia turnerifolia Fisch. & C.A. Mey. – herb, fl (Nov), R. Andreata 438; V. Ferreira 2111
Ficus arpazusa Casar. – tree, fr (Nov), R. Andreata 612
Ficus enormis (Mart. ex Miq.) Miq. – tree, fl (May, Jul), fr (May, Jul), R. Andreata 478, 593; C. Farney 738
Sorocea hilarii Gaudich. – tree, fl (Apr–May), fr (May), R. Andreata 436, 555, 571; V. Ferreira 2112

Myrtaceae (G.M. Barroso, M.C. Souza and M. Sobral)
Campomanesia schlechtendaliana (O. Berg) Nied., small tree, fl (sterile), R. Andreata 938
Eugenia jurujubensis Kiaersk. – shrub, fl (Oct–Nov), fr (Apr, Jul, Oct), R. Andreata 148, 149, 190, 324, 332, 340, 434, 483
Eugenia sulcata Spring. ex Mart. – tree, R. Andreata 960
Eugenia uniflora L. – tree, fr (Apr), R. Andreata 81, 495, 967, 974, 983
**Gomidesia gestasiana* (Cambess.) Legrand – shrub, fl (Nov), fr (Jul), R. Andreata 434
Gomidesia sonderiana O. Berg – shrub, fl (Nov), R. Andreata 307, 617
Marliera racemosa (Vell.) Kiaersk. – tree, R. Andreata 473
Myrcia insularis Gardner – shrub, fl (Jan), R. Andreata 387, 940
Myrcia racemosa (O. Berg) Kiaersk. – tree, fl (sterile), R. Andreata 926
Myrcia richardiana (O. Berg) Kiaersk. – tree, fl (Nov), fr (Jan), R. Andreata 388
Myrciaria floribunda (H. West ex Willd.) O. Berg – shrub, fr (Jan), R. Andreata 606, 968, 976
Myrciaria glazioviana (Kiaersk.) G. Barroso ex Sobral – shrub, fr (Sep), R. Andreata 499, 506
Psidium cattleyanum Sabine – tree, R. Andreata 622, 962
Indet.1 – tree, fl (sterile), R. Andreata 978

Myrsinaceae (M.F. Freitas)
Myrsine coriacea (Sw.) R. Br. ex Roem. – tree, fl (sterile), R. Andreata 939

Nyctaginaceae (C.F.C. Sá)
Bougainvillea spectabilis Willd. – shrub, fl (May), R. Andreata 551
Guapira opposita (Vell.) Reitz – shrub, fl (Jul–Sep), fr (May, Sep), R. Andreata 75, 80, 108, 486, 540, 559, 688, 698, 700, 950, 975, 989, 990; V. Ferreira 2240

Ochnaceae
Ouratea parviflora (DC.) Baill. – shrub, fl (Sep), fr (Sep), R. Andreata 521

Olacaceae
Heisteria perianthomega (Vell.) Sleumer – tree, fl (sterile), R. Andreata 720

Oxalidaceae
Oxalis barrelieri (L.) Small. – herb, fl (Aug, Dec), R. Andreata 13, 69
Oxalis fruticosa Raddi var. *daphniformis* (J.C.Mikan) Lourteig – sub-shrub, fl (Feb), R. Andreata 643; T. Plowman 13928
Oxalis sepium A. St.-Hil. – sub-shrub, fl (Nov), R. Andreata 305

Passifloraceae
**Passiflora racemosa* Brot. – climbing, fl (May, Jul–Aug, Oct–Jan), fr (May, Jul), R. Andreata 31, 121, 198, 459, 588, 921

Phytolacaceae
Gallesia integrifolia (Spreng.) Harms – tree, fl (sterile), R. Andreata 392
Microtea paniculata Moq. – herb, fl (Jan), V. Ferreira 2094
Petiveria alliacea L. – sub-shrub, fl (Aug, Dec), R. Andreata 20, 82; V. Ferreira 2096

Picramniaceae (J.R. Pirani)
**Picramnia grandifolia* Engl. – shrub, fl (Jul), R. Andreata 458

Piperaceae (E.F. Guimarães and D.M. Ferreira)
Peperomia corcovadensis Gardner – epiphytic, fl (Oct), R. Andreata 157
Peperomia incana (Haw.) Hook. – herb, fl (Sep, Nov), fr (Feb), R. Andreata 315, 649; T. Plowman 13934; G. Martinelli 8528
Peperomia tetraphylla (Forst.) Hook. & Arn. – epiphytic, fl (Nov), R. Andreata 201
Piper amalago L. var. *medium* (Jacq.) Yuncker – shrub, fl (Dec), R. Andreata 168, 923
Piper amplum Kunth – shrub, fl (Feb), fr (Feb), T. Plowman 12861

Plumbaginaceae
Plumbago scandens L. – climbing, fl (Nov), R. Andreata 325

Polygonaceae
Coccoloba confusa R.A. Howard – shrub, fl (Sep), R. Andreata 531
Ruprechtia laxiflora (Meisn.) Kuntze – tree, R. Andreata 952
Ruprechtia lundii (Meisn.) Kuntze – tree, fl (Sep), R. Andreata 718
Triplaris scandens (Casar.) Coccuci – tree, R. Andreata 918

Portulacaceae
Portulaca mucronata Link – herb, fl (Nov), R. Andreata 338, 535
Talinum patens (L.) Willd. – herb, fl (Oct–Nov), fr (Oct–Nov), R. Andreata 134, 177
Talinum racemosum (L.) Rohrb. – herb, fl (Aug), R. Andreata 66

Rhamnaceae
Reissekia smilacina Endl. – climbing, fl (Nov), R. Andreata 341

Rubiaceae (M. Gomes)
Alseis sp. – tree, fl (sterile), R. Andreata 678
Alseis floribunda Schott – tree, fl (Sep), fr (Jan–Sep), R. Andreata 717
Alseis involuta K. Schum. – tree, fl (Sep), fr (Jan–Sep, R. Andreata 358, 505, 980, 981
Chomelia brasiliensis A. Rich. – shrub, fl (Feb), fr (Feb), R. Andreata 428, 640; T. Plowman 13925
Coussarea sp. – shrub, fl (sterile), R. Andreata 972
**Coussarea capitata* (Benth.) Benth. & Hook. – tree, fl (Oct), R. Andreata 137

Coutarea hexandra (Jacq.) K. Schum. var. *fluminensis* K. Schum. – tree, fl (Apr), fr (Apr–May), R. Andreata 661, 691, 697
Faramea sitpulacea (Cham. & Schltdl.) DC. – shrub, fl (May, Sep), fr (May–Jul), R. Andreata 469,491, 557; C. Farney 737
**Faramea sp.* – tree, fl (Dec), R. Andreata 54; V. Ferreira 2110
Mitracarpus lhotzkyanus Cham. – herb, fl (Nov), R. Andreata 176
Posoqueria acutifolia Mart. – shrub, fr (Jan), R. Andreata 384
Psychotria brachyceras Müll. Arg. – shrub, fl (Oct–Dec), R. Andreata 30, 116, 171
**Psychotria stenocalyx* Müll. Arg. – shrub, fl (Oct–Nov), fr (Apr, Sep, Nov), R. Andreata 153, 418, 604; C. Farney 369
Randia armata (Sw.) DC. – shrub, fr (Apr), R. Andreata 441
Richardia brasiliensis Gomes – herb, fl (Jul), R. Andreata 16
Rudgea minor (Cham.) Standl. subsp. *calycina* (Benth.) Zappi – shrub, fr (Mar), H.C. Lima and F.C.P. Garcia 5027
Rudgea francavillana Müll. Arg. – shrub, fl (Sep), fr (Sep), R. Andreata 491, 507
**Rudgea interrupta* Benth. – shrub, fl (Jan, Sep, Nov), fr (Jan, Apr–May, Jul), R. Andreata 396, 420, 471, 474, 512, 572, 951; C. Farney 61; V. Ferreira 2103
Rudgea subcordata Müll. Arg. – shrub, fl (Oct), fr (Apr), R. Andreata 118
Simira sampaiona (Standly) Steyerm. – tree, fl (Oct), R. Andreata 124, 683, 723
Simira viridiflora (Allemão & Saldanha) Steyerm. – tree, fr (May, Jul, Nov), R. Andreata 195, 460, 574

Rutaceae (M. Emmerich and J.R. Pirani)
Almeidea rubra A. St.-Hil. – shrub, fl (May, Jul, Nov–Dec), fr (May, Aug, Nov), R. Andreata 53, 101, 467, 596; C. Farney 370
Conchocarpus ovatus A. St.-Hil. – shrub, fl (Nov), C. Farney 371
*Cusparia ovata (A. St.-Hil.) Tul., small tree, fl (Nov–Dec), fr (Apr), R. Andreata 197, 442, 158
Esenbeckia febrifuga (A. St.-Hil.) A. Juss. ex Mart. – tree, fr (Jul), R. Andreata 484
Galipea jasminiflora (A. St.-Hil.) Engl. – shrub, fl (Apr), fr (Apr), R. Andreata 416
Neoraputia alba (Nees & Mart.) Emmerich – tree, fr (Apr), R. Andreata 439

Sapindaceae (G.V. Somner)
Allophylus edulis (A. St.-Hil.) Radlk. – shrub, fl (Apr), R. Andreata 444
Allophylus heterophyllus Radlk. – shrub, fl (Oct), fr (Apr), R. Andreata 130, 440
Allophylus laevigatus Radlk. – shrub, fr (Oct), R. Andreata 109
Allophylus semidentatus Radlk. – tree, fl (Sep, Nov), R. Andreata 603, 942
Cupania sp. – tree, fl (sterile), R. Andreata 934
Cupania racemosa Radlk. – tree, fr (Jul), R. Andreata 374, 472, 728
Paullinia meliifolia A. Juss. – climbing, fr (Apr–May), R. Andreata 445, 598
Serjania corrupta Radlk. – climbing, fr (May), R. Andreata 589
Serjania cuspidata Cambess. – climbing, fr (Apr), R. Andreata 703
Serjania fuscifolia Radlk. – climbing, fl (Apr–May), fr (Apr), R. Andreata 417, 548
Urvillea stipitata Radlk. f. *stipitata* – climbing, fr (Apr), R. Andreata 668

Sapotaceae (M.H.D. Monteiro)
Chrysophyllum flexuosum Mart. – tree, fl (Jan, Apr), fr (Apr), R. Andreata 424; V. Ferreira 2105
Pouteria subsessilifolia Cronquist – tree, fl (Aug, Oct), fr (Oct), R. Andreata 133
Pouteria psamophila (Mart.) Radlk. – tree, fl (Oct), R. Andreata 161

Solanaceae (L.F.d'A.Carvalho)
Athenaea anonacea Sendtn. – shrub, fl (sterile), R. Andreata 355
Aureliana fasciculata (Vell.) Sendtn. var. *fasciculata*, small tree, fr (Oct), R. Andreata 114
Brunfelsia uniflora (Pohl) D. Don – shrub, fl (Aug), R. Andreata 100
Capsicum schottianum Sendtn. – shrub, fl (Sep), R. Andreata 522
Dyssochroma viridiflorum (Sims) Miers – shrub, fl (Aug–Sep), R. Andreata 103, 605
**Metternichia principis* Mikan var. *principis,* small tree, fl (Feb, Sep), fr (Jan, Jul, Nov), R. Andreata 352, 480, 508, 638, 677; T. Plowman 13923
Solanum alternatopinnatum Steud. – climbing, fl (Apr), fr (Apr), R. Andreata 413
Solanum americanum Mill. var. *americanum* – sub-shrub, fl (Nov), fr (Nov), R. Andreata 180
Solanum arenarium Sendtn. – shrub, fr (Jan), R. Andreata 404
Solanum argenteum Dunal – shrub, fl (Aug), fr (Aug–Nov), R. Andreata 71, 179
Solanum caavurana Vell. – shrub, fl (Nov), R. Andreata 328, 608
Solanum incarceratum Ruiz & Pav. – shrub, fl (Dec), R. Andreata 40
Solanum megalochiton Mart. var. *megalochiton* – climbing, fr (May), R. Andreata 597
Solanum melissarum Bohs – shrub, fl (Sep), R. Andreata 936
Solanum swartzianum Roem. & Schult. var. *swartzianum* – shrub, fl (Oct), R. Andreata 133
Solanum sp.1 – sub-shrub, fr (Jul), R. Andreata 490

Theophrastaceae
Clavija spinosa (Vell.) Mez – shrub, fr (Apr), R. Andreata 437

Trigoniaceae (E.F. Guimarães)
Trigonia eriosperma (Lam.) Fromm & Santos – sub-shrub, fl (Oct), fr (Aug), R. Andreata 76, 110

Turneraceae
**Turnera serrata* Vell. – sub-shrub, fl (Jun, Jul, Sep), fr (Aug, Sep, Nov), R. Andreata 84, 181, 497, 511, 710

Ulmaceae (J.P.P. Carauta)
Celtis brasiliensis (Gardner) Planch. – shrub, fl (Sep), fr (Jan, Mar, Sep), R. Andreata 516, 913; H.C. Lima and J.F.C.P. Garcia 5026

Urticaceae

Urera mitis (Vell.) Miq. – shrub, fl (Apr), R. Andreata 429

Verbenaceae

Aegiphila mediterranea Vell. – tree, fl (Aug), R. Andreata 78

Lantana sp. – sub-shrub, fl (Aug), fr (Sep), R. Andreata 74, 498

Stachytarpheta cf. maximilianii Schauer – herb, fl (Dec), R. Andreata 23

Stachytarpheta polyura Schauer – herb, fl (Oct), R. Andreata 146

Vitex polygama Cham. – shrub, fl (Sep, Nov), fr (Sep, Nov), R. Andreata 331, 543

Violaceae

Rinorea laevigata (Sol. ex Ging.) Hekking – shrub, fl (Aug, Sep), fr (Aug, Nov), R. Andreata 88, 532, 949

MONOCOTYLEDONS

Agavaceae

Furcraea gigantea Vent. – herb, fl (Feb), T. Plowman 12855

Alstromeriaceae

Alstroemeria caryophyllaea Jacq. – herb, fl (May, Jul, Aug), fr (May), R. Andreata 102, 412, 414, 462, 570, 573; C. Farney 732

Amaryllidaceae

Hyppeastrum reginae Herb. – herb, fl (Apr, Jul, Sep), R. Andreata 514, 946

Araceae (S.J. Mayo and M.A.C. Nadruz)

Anthurium coriaceum (Graham) G.Don – herb, fl (Sep), R. Andreata 343, 539

**Anthurium luschnathianum* Kunth – herb, fl (Feb, Nov), S. Mayo 607; V. Ferreira 2109

Anthurium olfersianum Kunth – herb, (Feb, Nov), R. Andreata 206; S. Mayo 606; V. Ferreira 2119

Anthurium pentaphyllum (Aubl.) G.Don – epiphytic, fl (Dec), R. Andreata 310

Anthurium scandens (Aubl.) Engl. subsp. *scandens* – epiphytic, fl (Nov), R. Andreata 207

Monstera adansonii Schott var. *klotzschiana* (Schott) Madison – herb, v.v.

Philodendron bipennifolium Schott – herb, S. Mayo 603

Philodendron corcovadense Kunth – herb, v.v.

Philodendron cordatum Kunth – herb, v.v.

Philodendron crassinervium Lindl. – herb, S. Mayo 605

**Philodendron speciosum* Schott ex Endl. – herb, S. Mayo 602

Arecaceae

Attalea sp. – tree, fl (Jan), R. Andreata 391

Syagrus romanzoffiana (Cham.) Glassman – tree, fl (May), fr (May), R. Andreata 553, 687, 690, 692, 693, 695, 699

Bromeliaceae (G. Martinelli)

Aechmea nudicaulis (L.) Griseb. var. *nudicaulis* – epiphytic, fl (Nov), R. Andreata 209

Aechmea purpureo-rosea (Hook.) Wawra – herb, v.v.

Aechmea ramosa Mart. ex Schult. var. *ramosa* – herb, fl (Jul), R. Andreata 465

Aechmea sphaerocephala Baker – herb, fl (Sep), G. Martinelli 8525

Alcantarea glazioviana (Lem.) Leme – herb, fl (Sep), R. Andreata 671; G. Martinelli 8527 (cultivated)

Billbergia pyramidalis (Sims) Lindl. var. *pyramidalis* – herb, fl (Nov–Dec), R. Andreata 65, 205

Bromelia antiacantha Bertol. – herb, fl (Sep), G. Martinelli 8523

Neoregelia ampullacea (E.Morren) L.B.Sm. – herb, fl (Jan), V. Ferreira 2114: G. Martinelli 8515

Neoregelia sarmentosa (Regel) L.B.Sm. – herb, fl (Nov), R. Andreata 204

Pitcairnia staminea Lodd. – herb, fl (Apr), R. Andreata 878

Tillandsia araujei Mez var. *araujei* – herb, R. Andreata 896; G. Martinelli 8521; T. Plowman 13933

Tillandsia dura Baker – herb, fl (Apr, Nov), R. Andreata 321; G. Martinelli 8519; T. Plowman 13924

Cannaceae (J.M.A. Braga)

Canna glauca L. – herb, fl (Nov), fr (Nov), R. Andreata 517

Commelinaceae

Dichorisandra thyrsiflora J.C. Mikan – herb, fl (Apr, Nov), R. Andreata 336

* *Siderasis fuscata* (Lodd.) H.E. Moore – herb, V. Ferreira 2104

Tradescantia zebrina Bosse – herb, v.v

Cyperaceae (C.S. Muniz)

Bulbostylis capilaris Clarke – herb, fl (Nov), R. Andreata 313

Cyperus coriifolius Boeck – herb, fl (Sep), R. Andreata 533

Cyperus diffusus Vahl – herb, fl (Dec), R. Andreata 18

Trilepis eximia (Clarke) Pfeiff. – herb, fl (Sep), R. Andreata 534

Dioscoreaceae

Dioscorea sp.1 – climbing, fl (Nov), R. Andreata 613

Dioscorea sp.2 – climbing, fl (Jan), fr (Jan), V. Ferreira 2120, 2122

Dioscorea sp.3 – climbing, fl (Nov), R. Andreata 150

Dioscorea glomerulata Hauman – climbing, fl (Jan), R. Andreata 406

Heliconiaceae (J.M.A. Braga)

Heliconia laneana Barreiros var. *laneana* – herb, fl (Oct), V. Ferreira 2116

Herreriaceae (R.C. Lopes)

Herreria salsaparrilha Mart. – climbing, fl (sterile), R. Andreata 730

Iridaceae

Neomarica sp. – herb, fl (Apr), R. Andreata 433

Marantaceae (J.M.A. Braga)

Calathea eichleri R.H. Petersen – herb, fl (Nov), fr (Jan), R. Andreata 680

Calathea truncata Lodd. – herb, fl (Nov), R. Andreata 45, 621

Maranta foliosa Körn. – herb, fl (Nov), fr (Apr), R. Andreata 342, 578

Orchidaceae (L. Toscano and F.C. Pinheiro)

Cyclopogon bicolor (Ker-Gawl) Schltr. – rupicolous, fl (Jul), T.B. Croat 53728; J.L. Moutinho 01

Cyrtopodium polyphyllum (Vell.) Pabst ex F. Barros – herb, fl (Sep), fr (Sep), R. Andreata 537

Epidendrum denticulatum Barb. Rodr. – herb, fl (Nov), R. Andreata 208
Epidendrum filicaule Lindl. – epiphytic rupicolous, fl (Nov, Dec), R. Andreata 337; F. Pinheiro195
Maxillaria marginata (Lindl.) Fenzl – rupicolous, fl (Oct), F. Pinheiro 181
Octomeria alpina Barb. Rodr. – epiphytic, fl (Sep), F. Pinheiro 173
Oncidium fimbriatum Lindl. – epiphytic rupicolous, fl (Oct), F. Pinheiro 180
Oncidium pumilum Lindl. – epiphytic, fl (Apr), F. Pinheiro 202
Pleurothallis grobyi Lindl. – rupicolous, fl (Feb, Mar), F. Pinheiro 144; L.O.F. Souza 41
Pleurothallis pardipes Rchb. f. – epiphytic, fl (Mar), F. Pinheiro & M. Guerra s/n
Pleurothallis saundersiana Rchb. f. – epiphytic rupicolous, fl (Mar), F. Pinheiro 143
Sophronitis cernua Lindl. – epiphytic, v.v.

Poaceae (A.G.Burman)
Bambusa sp. – herb, fl (Oct), R. Andreata 920
Ichnanthus sp. – herb, fl (Oct), R. Andreata 126
Olyra brasiliensis (Bertol.) Spreng. – herb, fl (Oct), R. Andreata 156
Pennisetum setosum (Sw.) Rich. – herb, fl (Oct), R. Andreata 145
Stipa latifolia (L.) Raspail – herb, fl (Oct–Nov), R. Andreata 319

Smilacaceae
Smilax sp. – climbing, fr (Oct), R. Andreata 140
Smilax quinquenervia Vell. – climbing, sterile, R. Andreata 151, 554
Smilax subsessiliflora Duham. – climbing, fl (Sep), fr (Apr), R. Andreata 95, 159, 167, 200, 435, 518, 527

Velloziaceae
Vellozia candida J.C. Mikan – herb, fl (Apr), R. Andreata 881

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LA FAMILIA NYMPHAEACEAE EN EL ESTADO DE NUEVO LEÓN, MÉXICO

Carlos Velazco-Macías

Parques y Vida Silvestre de Nuevo León
Calle París # 343, Col. Mirador, C.P. 64070
Monterrey, Nuevo León, MÉXICO
carlos.velazco@gmail.com

Rahim Foroughbakhch Pournavab, Marco A. Alvarado Vázquez, y Glafiro J. Alanis Flores

Facultad de Ciencias Biológicas, U.A.N.L.
San Nicolás de los Garza
Nuevo León, MÉXICO

RESUMEN

Existen grandes vacíos en el conocimiento florístico del estado de Nuevo León situado en el noreste de México, el presente estudio pretende contribuir a llenar dichos vacíos al realizar una revisión de las especies de la familia Nymphaeaceae en esta entidad. A través de una revisión bibliográfica y de ejemplares de herbario se obtuvieron registros considerados como históricos, además a través de visitas de campo a 17 localidades con hábitat potencial para la ocurrencia de esta familia, se corroboró la presencia de especies de esta familia y se identificaron nuevos registros. Se encontró que para Nuevo León, los registros de literatura y herbario señalan solamente 2 géneros (*Nuphar* y *Nymphaea*) y dos especies (*Nuphar advena* y *Nymphaea ampla*) en 2 localidades para el género *Nuphar* y 3 localidades para el género *Nymphaea*, mientras que el trabajo de campo mostró dos especies no reportadas para Nuevo León (*Nymphaea mexicana* y *N. elegans*) cada una en una sola localidad, *N. ampla* se encontró además en dos localidades no reportadas previamente y no fue posible localizarla en ninguna de las tres localidades consideradas como históricas según los ejemplares de herbario revisados, de manera similar *Nuphar advena* desapareció de una de las localidades históricas reportadas. Dada la rápida reducción de los humedales en Nuevo León, se estima que esta familia puede desaparecer del estado en un lapso no mayor a 10 años.

ABSTRACT

There are gaps in our existing knowledge of the floristics of the State of Nuevo Leon in northeastern Mexico. This paper updates the current state of floristic knowledge for the family Nymphaeaceae. Bibliographic and herbarium work was conducted along with extensive field work at 17 localities. New collections and herbarium studies document two genera (*Nuphar* and *Nymphaea*) for Nuevo León. Two new state records are documented: *Nymphaea elegans* and *N. mexicana*, each at a single locality. *Nymphaea ampla* was collected at two new localities while it is now absent at three historical localities based on herbarium specimens. Also, *Nuphar advena* was eradicated from one of the historical sites. Given the rate of habitat destruction and loss of wetlands in Nuevo León, we estimate members of the Nymphaeaceae could disappear from Nuevo León in the next 10 years or less.

INTRODUCCIÓN

El estado de Nuevo León no cuenta con un listado florístico actualizado, para el año de 1965, se registraban un total de 1,296 especies, entre plantas nativas, cultivadas y adventicias, distribuidas en 657 géneros y 148 familias de plantas vasculares (Rojas-Mendoza 1965); otras estimaciones proponen cerca de 2,400 especies de flora vascular (Alanis-Flores et al. 1996). De manera puntual, la vegetación acuática o semiacuática ha recibido poca o ninguna atención en los estudios florísticos, se conoce solamente un estudio de la Presa Rodrigo Gómez y sus afluentes en el municipio de Santiago (Moreno 1984).

Para la familia Nymphaeaceae en Nuevo León, solamente existen reportes en la literatura de *Nymphaea odorata* y *N. mexicana*, ambas son mencionadas como especies cultivadas (Rojas Mendoza 1965), sin que existan registros de herbario de estas especies hasta el momento. La única especie de la familia Nymphaeaceae que ha sido publicada de manera formal con respaldo de un ejemplar herborizado es *N. ampla* (Lot et al. 1986; Novelo y Bonilla 1999). De estados vecinos como Coahuila, se reporta solo *N. ampla* (Villarreal-Quintanilla 2001; Villarreal-Quintanilla et al. 2006), mientras que para Tamaulipas se reportan *Nuphar luteum*, *Nymphaea ampla*, *N. elegans* *N. jamesoniana* y *N. amazonum* (Lot et al. 1986; Martínez y Novelo 1993; y Mora-Olivo y Villaseñor 2007), y en el estado de Texas, en Estados Unidos de Norteamérica se reportan 4 especies de *Nymphaea*: *N. ampla*, *N. mexicana*, *N. odorata* y *N. elegans*, además de *Nuphar luteum* subsp. *macrophyllum* (Correll y Johnston 1979; Wiersema y Hellquist 1997). Cabe mencionar que para el caso particular del género *Nuphar*, ha existido una gran controversia en

lo referente a la aplicación del epíteto específico, ya que *N. luteum* es de origen europeo, mientras que a través de trabajos genéticos y moleculares las especies americanas han mostrado una separación de las especies del viejo mundo, se aplica el nombre *N. advena* a los ejemplares reportados en trabajos recientes (Wiersema y Hellquist 1997).

El objetivo del presente trabajo es documentar los registros de la familia Nymphaeaceae en el estado de Nuevo León, así como conocer el rango de distribución actual de las especies presentes como una contribución al conocimiento florístico.

METODOLOGÍA

Área de estudio

El estado de Nuevo León se localiza en la parte noreste de México, entre los 98° 17' y 101° 07' de longitud oeste, y los 23° 06' y 27° 50' de latitud norte. Limita al norte con los Estados Unidos de América y los estados de Coahuila y Tamaulipas; hacia el poniente limita con los estados de Coahuila, San Luís Potosí y Zacatecas, mientras que hacia el sur colinda con San Luis Potosí y Tamaulipas, con este ultimo también comparte la totalidad de su límite oriental (Fig. 1).Su superficie es de 64, 081.94 km^2, las elevaciones van desde los 200 a los 3,700 m sobre el nivel del mar. Se presentan porciones importantes de tres regiones fisiográficas de México, la Sierra Madre Oriental, la Gran Llanura de Norteamérica y la Planicie Costera del Golfo (Alanís-Flores et al. 1996). Predominan los climas semisecos extremosos, la precipitación pluvial es variable, el promedio general va desde los 300 a los 600 mm de precipitación anual. Los climas secos y semisecos se distribuyen principalmente de la región nororiental y en la región suroccidental, ambas áreas están separadas por la Sierra Madre Oriental, siento en esta última donde además se presentan climas, semicálidos, templados y semifrios en la zona centro y sur de la entidad (INEGI 1986). La vegetación se compone principalmente de matorrales desérticos y semidesérticos de diversa composición florística, en la región de la Sierra Madre se presentan bosques con distintas asociaciones de encinos, pinos, y coníferas. En menor grado se presentan sucesiones edafológicas como vegetación gypsófila o vegetación halófita; la vegetación acuática solamente se encuentra registrada como bosque de galería en algunas corrientes de agua permanentes del estado (Treviño-Garza et al. 2001). Si bien existen en Nuevo León numerosas áreas con hábitats de tipo lótico, como escurrimientos temporales en el área de la Sierra Madre Oriental y vegetación riparia, son pocos los ríos que actualmente mantienen el flujo de agua a lo largo del año; por otra parte los ecosistemas lénticos que son el hábitat potencial para la familia Nymphaeaceae, son sumamente escasos, algunos han desaparecido en los municipios de Galeana y Aramberri por el uso desmedido del recuso hídrico en las actividades agropecuarias, otros como en el caso del Cañón de la Huasteca en el municipio de Santa Catarina, han sido canalizados para el abastecimiento de la zona metropolitana de Monterrey, dejando en la actualidad solo unos cuantos sitios restantes en el estado para el desarrollo de comunidades de vegetación acuática y semiacuática.

Métodos

Primeramente se realizó una revisión y consulta bibliográfica para la búsqueda de registros de la familia Nymphaeaceae en Nuevo León, además de consultas en las bases de datos de los siguientes herbarios: TEX, LL, UNL, MO, NY y el herbario de George B. Hinton para la búsqueda de ejemplares documentados de la familia.

Se realizó trabajo de campo en las diversas localidades que resultaron de la búsqueda de ejemplares de herbario para corroborar la presencia de las especies en la actualidad, en total se realizaron visitas a 17 localidades con hábitat potencial en diversos municipios de Nuevo León para documentar los sitos de distribución de las especies (Tabla 1). Las diagnosis de la familia, géneros y especies, así como la identificación de los ejemplares colectados están basadas en Zomlefer 1994; Novelo y Bonilla 1999; Calderón y Rzedowski 2001; Correll y Johnston 1979; Wiersema y Hellquist 1997.

El material colectado, fue herborizado y depositado en el herbario de la Facultad de Ciencias

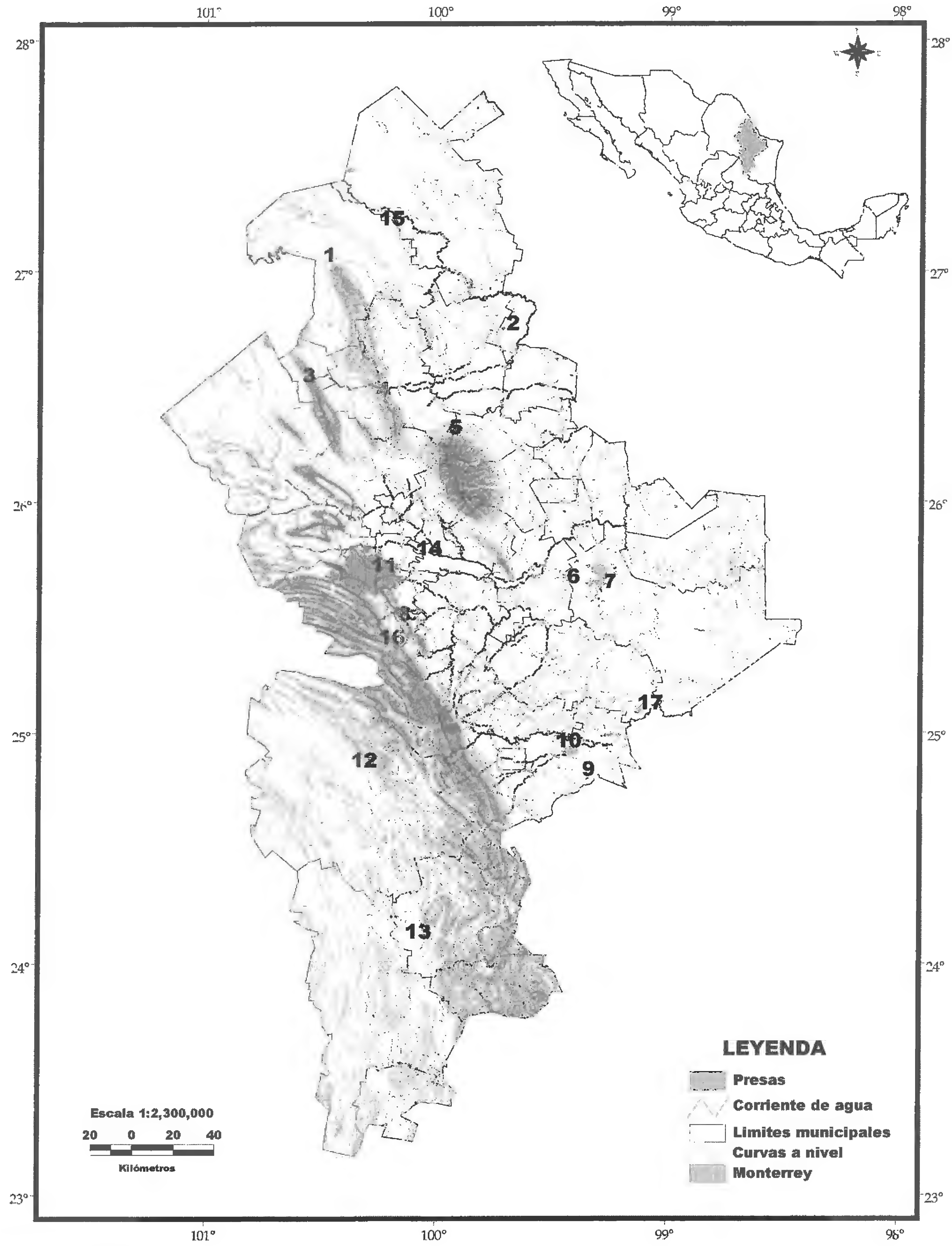

Fig. 1. Ubicación del estado de Nuevo León y sitios de muestreo del presente estudio.

Biológicas de la Universidad Autónoma de Nuevo León (UNL) siguiendo las recomendaciones de Lot y Chiang, 1986 para el montaje y herborización de ejemplares botánicos.

RESULTADOS

En el estado la familia está representada por 2 géneros (*Nymphaea* y *Nuphar*) y 4 especies (*Nymphaea ampla*, *N. elegans*, *N. mexicana* y *Nuphar advena*), las cuales se distribuyen en 4 municipios en la Planicie Costera del Golfo y los límites con la Sierra Madre Oriental (Figs. 1–3).

Los registros de herbario muestran que se han extirpado diversas poblaciones, *Nuphar advena* ha desparecido del municipio de Paras, mientas que *Nymphaea ampla* se ha eliminado de diversos hábitats en los municipios de Bustamante, Lampazos de Naranjo y Apodaca (Tabla 1).

Las 17 localidades visitadas se muestran en la Tabla 1, en donde se muestra también el estado actual de cada una de ellas, y la presencia o ausencia de la familia.

Familia Nymphaeaceae Salisb.

Plantas herbáceas, acuáticas, perennes, rizomatosas, a veces acaules; hojas simples, usualmente enteras, alternas, con venación palmada o pinnada, saliendo directamente del rizoma, largamente pecioladas, láminas flotantes o expuestas fuera del agua; flores solitarias, axilares, actinomórficas, perfectas, hipoginias, periginias o algunas veces epiginias, comúnmente grandes y vistosas, flotantes o sobresaliendo del espejo de agua, provistas de pedúnculos largos; cáliz usualmente de 4 a 6 sépalos, libres, algunas veces petaloides, imbricados; corola con pétalos de 3 a muchos, dispuestos numerosas series, los cuales a menudo no se diferencian claramente de los estambres, transformándose de forma gradual en estaminodios o estambres, algunas veces con nectarios abaxiales, de colores vistosos como amarillo, rojo, azul o blanco, imbricados; androceo compuesto de 3 a numerosos estambres laminares y arreglados de manera espiral, filamentos lineares o petaloides, pobremente diferenciados de las anteras, libres o unidos a los pétalos, anteras con dehiscencia longitudinal intrusa o extrosa; gineceo apocárpico o sincarpico, con 3 o más carpelos, óvulos numerosos en cada lóculo, anátropos, placentación lateral o lamelar, estilos ausentes, estigma(s) unidos y formando un disco con el mismo número de rayos que los carpelos, área recpetacular en toda la superficie discoidal o solamente restringida a las áreas con rayos; fruto parecido a una baya, esponjoso, con dehiscencia irregular (debido a la expansión producida por el mucílago que rodea a las semillas), semillas pequeñas, usualmente operculadas, a menudo con arilo, endospermo escaso, perispermo copioso.

Familia con una amplia distribución mundial, desde las regiones frías y templadas en el hemisferio norte hasta el trópico, habitando cuerpos lénticos de agua dulce; se incluyen en la familia 6 géneros con alrededor de entre 50 y 66 especies. En México se presentan 2 géneros con entre 11 y 12 especies. En el pasado se incluían en esta familia a los miembros de Cabombaceae y Nelumbonaceae, las cuales ahora se encuentra segregadas gracias a estudios moleculares.

CLAVES PARA LOS GÉNEROS DE LA FAMILIA NYMPHAEACEAE EN NUEVO LEÓN

1. Perianto subgloboso de seis sépalos cóncavos de color amarillos (a veces teñidos de verde o rojo) y numerosos pétalos escuamiformes o estamiformes insertados con los estambres en un receptáculo por debajo del ovario; carpelos completamente unidos, estigmas radiados y sésiles en un disco; semillas sin arilo________ **1. Nuphar**
1. Perianto muy amplio, compuesto de cuatro sépalos y numerosos pétalos (más de 10) muy vistosos, de colores blanco, amarillo o azul; carpelos hundidos en un receptáculo carnoso con forma de copa o hipantio en la superficie externa en la cual los pétalos y estambres están insertados, estirados hacia arriba en forma de proyecciones delgadas y curvas (estilos carpelares); semillas con arilo ________________________ **2. Nymphaea**

1. **Nuphar** Sm.

Nymphozanthus Rich.

Plantas herbáceas, acuáticas, con rizomas, sin estolones; hojas flotantes, sumergidas o emergentes, desde

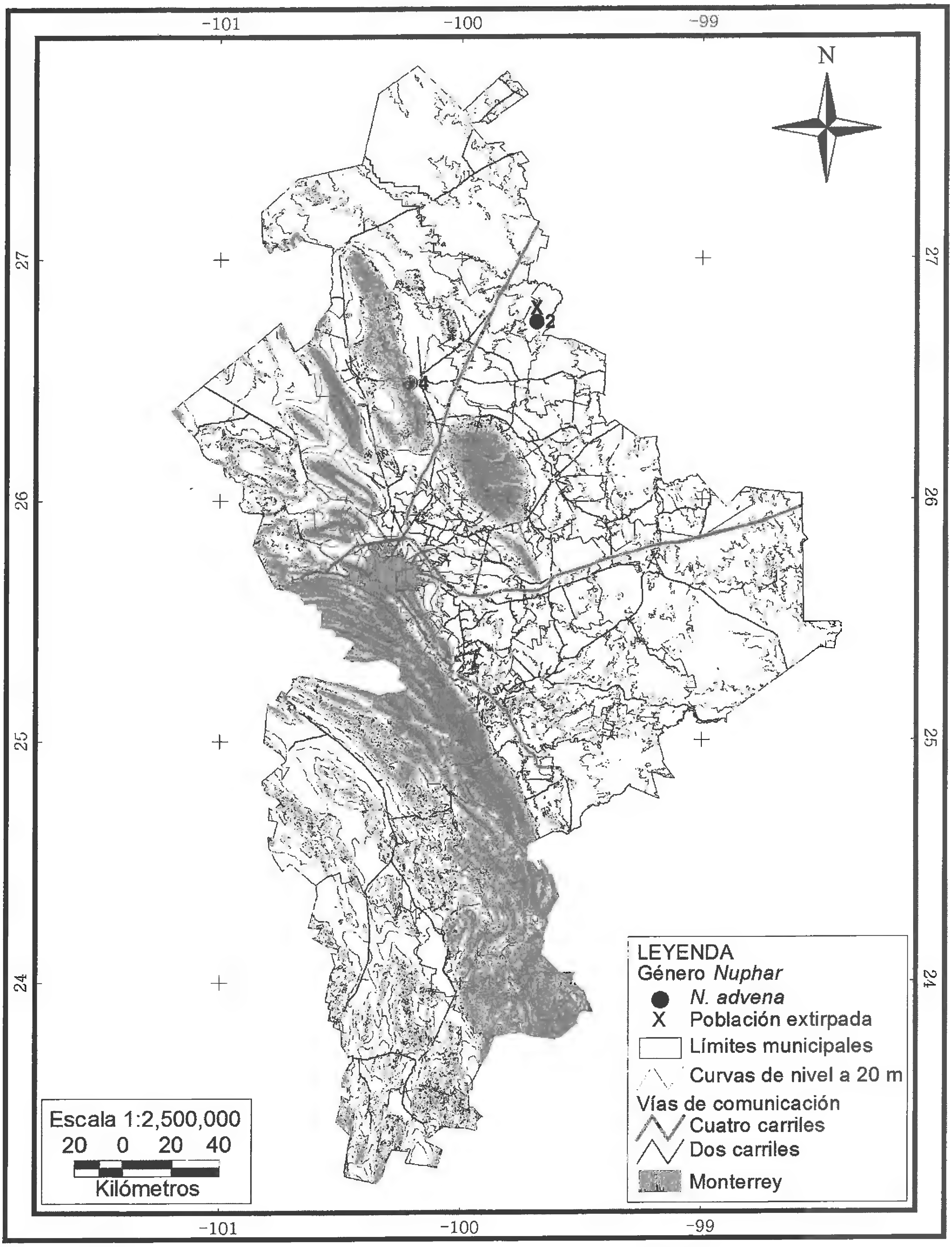

Fig. 2. Distribución del género *Nuphar* en Nuevo León, los números indican las localidades referidas en la Tabla 1.

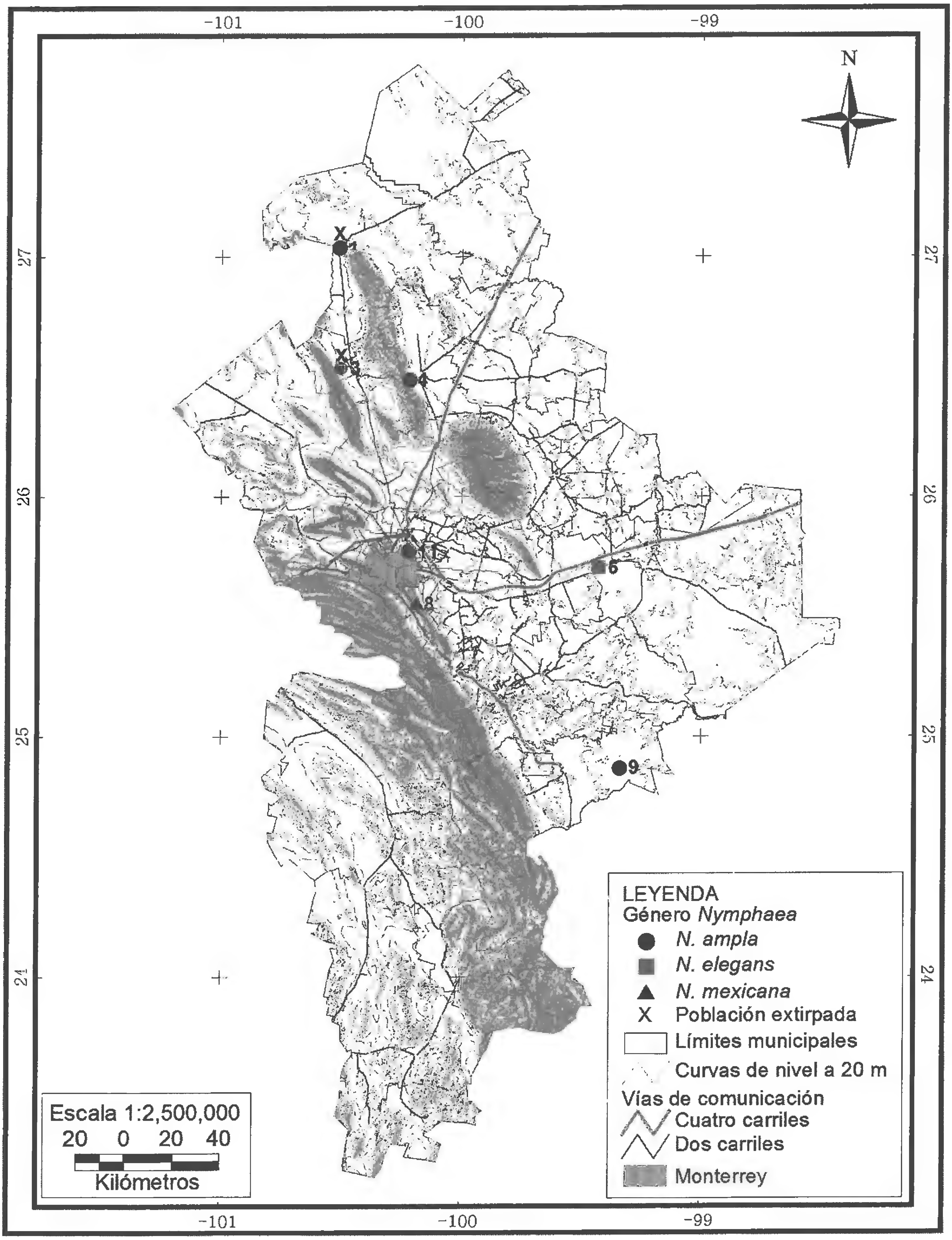

FIG. 3. Distribución del género *Nymphaea* en Nuevo León, los números indican las localidades referidas en la Tabla 1.

Tabla 1. Localidades visitadas, su estado de conservación y presencia de la familia Nymphaeaceae.

Localidad	Municipio	Estado de conservación/ Uso actual	Presencia de la familia
Ojo de agua de Lampazos	Lampazos de Naranjo	Impactado / Uso turístico recreativo	Histórica, extirpada en la actualidad
Presa de Paras	Paras	Impactado / Uso local riego y abrevadero	Histórica, extirpada en la actualidad
Ojo de agua de Bustamante	Bustamante	Impactado / Uso turístico recreativo	Histórica, extirpada en la actualidad
Ojo de agua de Sabinas Hidalgo	Sabinas Hidalgo	Buen estado / Uso turístico recreativo	Histórica, presente en la actualidad
Presa de Sombreretillo	Sabinas Hidalgo	Buen estado / Uso turístico recreativo	Sin registros, no presente en la actualidad
Pantano de China	China	Buen estado / Sin uso aparente	Sin registros, presente en la actualidad
Presa El Cuchillo	China	Buen estado / Sin uso aparente	Sin registros, no presente en la actualidad
Cañón de San Ana	Benito Juárez	Impactado / Uso local riego y abrevadero	Sin registros, no presente en la actualidad
Baño de San Ignacio	Linares	Buen estado / Uso local riego y abrevadero	Sin registros, presente en la actualidad
Presa Cerro Prieto	Linares	Buen estado / Uso turístico recreativo	Sin registros, no presente en la actualidad
Ojo de agua de Apodaca	Apodaca	Impactado / Uso turístico recreativo	Histórica, extirpada en la actualidad
Manantial del Potosí	Galeana	Desecado en su totalidad	Sin registros
Manantial de San Juan y Puentes	Aramberri	Desecado en su totalidad	Sin registros
Ojo de agua de Pesquería	Pesquería	Impactado / Uso turístico recreativo	Sin registros, no presente en la actualidad
Ojo de agua de Anahuac	Anahuac	Impactado / Uso turístico recreativo	Sin registros, no presente en la actualidad
Presa Rodrigo Gómez (La Boca)	Santiago	Impactado / Uso turístico recreativo	Sin registros, no presente en la actualidad
Presa Los Mimbres	Montemorelos	Impactado / Uso turístico recreativo	Sin registros, no presente en la actualidad

orbiculares a lineares, lóbulos basales de divergentes a traslapados, márgenes enteros, el ápice del lóbulo de delgadamente obtuso a ampliamente redondeado, venación primaria mayormente pinnada; flores flotantes o sobresaliendo del espejo de agua, diurnas, de forma casi globosa en la antesis; sépalos de 5 a 9, amarillos a verdes en la parte externa a menudo con tintes rojizos, oblongos u obovados hasta algo orbiculares; pétalos numerosos, con arreglo espiral, inconspicuos, a menudo asemejando a los estambres; estambres amarillos o rojizos, insertos por debajo del ovario, recurvados cuando dehiscentes, apéndice conectivo distal ausente; ovario mas grande que pétalos y estambres, disco estigmático con margen entero crenado o dentado; frutos naciendo en pedúnculos rectos, semillas ovides, arilo ausente.

Se distribuye en América, Europa y Asia; un genero complicado desde el punto de vista taxonómico, muchas veces se presentan híbridos y rasgos intermedios entre poblaciones; se reconocen entre 10 y 12 especies, las cuales a algunas veces se tratan como subespecies, en México ocurren 1 o 2 especies dependiendo del sistema de clasificación que se adopte. En Nuevo León ocurre solo una especie.

1. Nuphar advena (Aiton) W.T. Aiton

Nymphozanthus advena (Aiton) Fernald

Nymphaea advena Aiton

Plantas herbáceas acuáticas, enraizadas, rizomas de entre 5 y 10 cm. de diámetro; hojas comúnmente emergiendo del agua, pecíolo terado, o adaxialmente algo aplanado, laminas adaxial y abaxialmente de color verde, ampliamente ovadas hasta casi orbiculares, de 1 a 2 veces más larga que ancha, de hasta 40 cm de largo por hasta 30 cm de ancho, seno de la lámina de 1/3 a ½ de la longitud de la nervadura central, los lóbulos se sobreponen o son divergentes, a menudo formando un ángulo de 90° o mayor, la superficie abaxial de la lámina es glabra a escasamente pubescente; flores de hasta 5 cm de diámetro; sépalos comúnmente 6, abaxialmente de color verde y de color amarillo en la superficie adaxial, a veces teñidos de rojo hacia la base, pétalos oblongos y gruesos; anteras de 3 a 7 mm, más largas que los filamentos, disco estigmático verde, algunas veces rojizo, de 13 a 25 mm de diámetro, entero o crenado, rayos estigmáticos de 9 a 23, lineares a lanceolados, terminando de 1 a 3 mm desde el margen del disco; fruto verde, ovoide, con costillas poco prominentes algunas veces, algo constreñido por debajo del disco estigmático, semillas de 3 a 6 mm de largo.

Se ha registrado la desaparición de la población del municipio de Paras, esto es atribuible a la desecación de los cuerpos de agua en algunas temporadas; las poblaciones del municipio de Sabinas Hidalgo son abundantes, sin embargo se le considera como una especie problemática por su rápido crecimiento y puede llegar a cubrir rápidamente grandes extensiones de cuerpos de agua someros.

Ejemplares examinados: **MÉXICO. Nuevo León. Municipio de Sabinas Hidalgo:** Río Sabinas, 1 May 1981, *Garza M, N. s.n.* (UNL); Parque La Turbina, 26°29'12"-100°12'54°, 320 msnm, 28 Jun 2007, *Velazco-Macías 069* (UNL). **Municipio de Paras:** Presa Paras, 4 Oct 1971, *Valdez González, A. s.n.* (UNL).

2. Nymphaea L.

Castalia Salisb.

Plantas herbáceas perennes, acuáticas, rizomas rastreros; hojas largamente pecioladas, lamina flotante o expuesta fuera del agua, algo suborbicular, peltada o hendida de manera profunda en la base, borde de la lámina entero o dentado- ondulado; flores solitarias, con pedúnculo largo, flotantes o saliendo fuera del agua, muy conspicuas, de apertura diurna, algunas veces con un tenue olor agradable; sépalos 4; pétalos muy numerosos, trasformándose de manera gradual en estambres o estaminodios, colocados en varias series; filamentos petaloideos, los exteriores anchos, con anteras pequeñas, los interiores angostos con anteras más grandes; carpelos hundidos en un receptáculo carnoso, formando con él, un ovario carnosos semi-ínfero, estigma discoideo con pocos o muchos rayos, óvulos numerosos, pegados a las paredes divisorias de los lóbulos; fruto madurando debajo del agua, de consistencia esponjosa, globoso u ovoide, a veces cubierto con las bases persistentes de pétalos y estambres, semillas numerosas envueltas en un arilo en forma de saco.

Se estima que existen unas 50 especies distribuidas de manera amplia en todas las regiones tropicales y subtropicales. Utilizadas como plantas ornamentales, algunas especies se han considerado como invasivas. En México existen alrededor de 11 especies, distribuidas prácticamente en todos los estados, de manera particular en aquellos de afinidad tropical; en Nuevo león se presentan 3 especies.

CLAVES PARA LAS ESPECIES DEL GÉNERO *NYMPHAEA* EN NUEVO LEÓN

1. Pétalos de color amarillo; sépalos de color verde claro, sin marcas oscuras en la parte externa; flores con un leve olor agradable ____ **1. Nymphaea mexicana**
1. Pétalos de color blanco o azul-purpúreo; sépalos de color verde claro o amarillentos, con manchas obscuras o líneas en parte externa; flores sin olor.
    2. Pétalos de color blanco; bordes de las hojas ondulado-aserrados ____ **2. N. ampla**
    2. Pétalos de color azul blanquecino o azul purpúreo; borde de las hojas liso ____ **3. N. elegans**

1. Nymphaea mexicana Zucc.

Castalia flava (Leitner) Greene
Nymphaea flava Leitner

Rizoma recto y alargado, de color café, verrucoso, estolonífero en el ápice; pecíolo de hasta 1 m de largo, láminas flotantes, glabras, ovadas, de hasta 20 cm de largo o ancho, ápice no escotado, borde liso o ligeramente ondulado, base escotada, venación radiada, sin patrón en forma de telaraña, haz de color verde, envés de color café o café –rojizo; flores diurnas, comúnmente flotantes, algunas veces sobresaliendo del agua, de hasta 13 cm de diámetro; sépalos cuatro, lanceolados y agudos en el ápice, de hasta 8 cm de largo, de color verde claro, sin manchas en la parte externa, amarillo claro en la parte interna; pétalos de 30 a 40, de color amarillo o amarillo claro, de hasta 6 cm de largo por 1 cm o menos de ancho; estambres de 40 a 60, de color amarillo, apéndice conectivo diminuto o ausente, filamentos más anchos por debajo de la mitad, más largo que la antera; estilos de 7 a 9; fruto ovoide de hasta 2.5 cm de largo; semillas globosas de hasta 5 mm de diámetro.

Florecen principalmente en verano, pero se pueden encontrar en floración durante todo el año; se distribuye en Estados Unidos en los estados de Oklahoma, Alabama, Florida, Georgia, Louisiana, Mississipi, Carolina del Norte, Carolina del sur, Texas y Arizona; en México se registra para el Distrito Federal y los estados de Hidalgo, México y Michoacán, considerada en algunos lugares como una planta invasora.

En Nuevo León solo se ha encontrado en una localidad en el municipio de Benito Juárez, en una represa artificial en el Cañón de Santa Ana, municipio de Benito Juárez.

Ejemplares examinados: **MÉXICO. Nuevo León. Municipio de Benito Juárez:** Cañón de Santa Ana, 25°33'12" – 100°11'09", 590 msnm, 15 May 2007, *Velazco-Macías 063* (UNL).

2. **Nymphaea ampla** (Salisb.) DC.

Castalia ampla Salisb.

Rizoma recto, no ramificado, sin estolones; pecíolo de hasta 1 m de largo glabro, láminas flotantes, haz de color verde, envés de color purpúreo frecuentemente manchado, de forma ovoide, y hasta 45 cm de largo por ancho, márgenes dentados a espinoso-dentados, venación radial, sin un patrón en forma de telaraña, superficie glabra; flores emergiendo del agua, de hasta 18 cm de diámetro, diurnas; sépalos cuatro, lado abaxial de color verde claro con manchas o líneas de color oscuro, lado adaxial de color blanco sin manchas; pétalos de 12 a 21 de color blanco; estambres de 50 a 190, amarillos, los más exteriores con un apéndice conectivo proyectándose de 3 a 10 mm más allá de la antera, filamentos ensanchándose por debajo de la mitad, comúnmente iguales o más cortos que las anteras; pistilo con 14 a 25 lóculos, apéndices al margen del disco estigmático cortamente triangulares hasta 3 mm; semillas globosas a elipsoides.

Florece durante todo el año pero principalmente en verano; presenta una amplia distribución, en Estados Unidos se ha reportado para los estados de Florida y Texas, mientras que para México se ha presenta en los estados de Coahuila, Nuevo León, San Luís Potosí, Tamaulipas, Colima, Guerrero, Jalisco, Michoacán, Oaxaca, Puebla, Querétaro, Veracruz, Campeche, Chiapas, Quintana Roo, Tabasco y Yucatán, se ha reportado también para Belice, Costa Rica, El Salvador, Guatemala, Honduras, Nicaragua, Panamá, Islas Caimán, Cuba, Republica Dominicana, Haití y Jamaica.

En el estado de Nuevo León, es la especie con distribución más amplia, ya que se ha colectado para 5 diferentes municipios en el norte y centro del estado, aunque en la actualidad solamente se presenta en 2 de ellos, Sabinas Hidalgo y Linares.

Ejemplares examinados: **MÉXICO. Nuevo León. Municipio de Apodaca:** Ojo de agua de Apodaca, 22 Oct 1971, *Valdez González s.n.* (UNL). **Municipio de Bustamante:** 1 Ago 1938, *H. LeSuerur, s.n.* (TEX). **Municipio de Lampazos de Naranjo**: Río Candela, cerca de la cabecera municipal, 290 msnm, 22 Jul 1980, *Briones V. 233* (UNL). **Municipio de Linares:** Baño de San Ignacio, 24°51'56"- 99°20'10", 240 msnm, 13 Jun 2007, *Velazco-Macías 068* (UNL). **Municipio de Sabinas Hidalgo:** Parque La Turbina, 26°29'12"-100°12'54", 320 msnm, 28 Jun 2007, *Velazco-Macías 070* (UNL).

3. **Nymphaea elegans** Hook.

Castalia elegans (Hook.) Greene

Rizoma recto, no ramificado, sin estolones; pecíolo de hasta 1 m de largo, glabro, láminas flotantes, haz de color verde, envés de color purpúreo, de forma ovoide, de hasta 25 x 30 cm, márgenes enteros o algo ondulados, venación radial y prominentemente central, sin un patrón en forma de telaraña, superficie glabra; flores diurnas, emergiendo del agua, de hasta 13 cm de diámetro; sépalos cuatro, lado abaxial de color verde claro con manchas o líneas de color oscuro, lado adaxial de color blanco sin manchas; pétalos hasta 27 de color púrpura claro hasta casi blancos; estambres de 55 a 145, amarillos, apéndice conectivo proyectándose 1 mm (raramente más), más allá de la antera, filamentos ensanchándose por debajo de la mitad, más cortos que las anteras; pistilo con 12 a 20 lóculos, apéndices al margen del disco estigmático triangulares de 1 mm o menos, semillas casi globosas.

Florece de primavera a otoño; presenta una amplia distribución, en Estados Unidos se encuentra en Florida, Louisiana y Texas, en México se ha reportado en Sinaloa, Sonora, Tamaulipas, Guerrero, Jalisco, Morelos, Nayarit, Oaxaca y Veracruz, también se ha reportada para las Bahamas y Argentina.

En el estado de Nuevo León se ha encontrado solamente en una localidad en el municipio de China, sobre la carretera libre Monterrey – Reynosa, en áreas inundables dominadas por *Acacia farnesiana* y ciperáceas diversas.

Ejemplares examinados: **MEXICO. Nuevo León. Municipio de China:** Carretera libre Monterrey-Reynosa, km. 93, 25°42'08"- 99°25'47", 323 msnm, 7 Nov 2006, *Velazco-Macías s.n.* (UNL),

DISCUSIÓN

Se identifican dos situaciones preocupantes, en primera instancia, el presente estudio pone de manifiesto la reducción en la distribución geográfica de las especies de flora asociadas a cuerpos de agua, por mencionar un ejemplo, *N. ampla*, ha desaparecido de 3 localidades en las cuales estaba documentada con ejemplares colectados entre los años de 1938 y 1980, esta situación es atribuible en gran parte a la desecación intencional de los cuerpos de agua, el uso de grandes volúmenes de agua subterránea y superficial para riego y consumo humano (Rzedowski 1978), de manera adicional a estos factores, el uso recreativo en algunas zonas ha sido determinante en la modificación del hábitat y la desaparición de especies; así de un total de 17 localidades visitadas en el estado, solamente 4 albergan poblaciones de esta familia. Una segunda situación de importancia, es la poca representación de esta en los herbarios consultados, esto se pone de manifiesto al contabilizar solamente 4 ejemplares herborizados y 1 una especie reportada en la literatura, aún más se contabilizan un total de 11 especies de angiospermas acuáticas estrictas registradas para Nuevo León (Lot et al. 1998), siendo los miembros de esta familia, especies llamativas y conspicuas por sus características fisonómicas, es difícil justificar el poco interés por representar esta familia en las colecciones botánicas, aún asi, el presente estudio arroja que dos de las especies reportadas (*Nymphaea elegans* y *N. mexicana*) se presentan como nuevos registros para Nuevo León.

En base a las colectas históricas, así como lo observado en las distintas localidades visitadas, en donde se ha observado un alto impacto por actividades del hombre e incluso la total desaparición del hábitat en algunas localidades, se estimaría que en un lapso de 10 años las especies aquí reportadas puedan desaparecer del hábitat restante en el estado de Nuevo León, esta preocupación ha sido denotada en otros estudios, tales como el de Novelo y Bonilla (1999) quienes señalan a *Nymphaea ampla* como "rara en la región de estudio y por lo tanto vulnerable a la extinción," esto a pesar de ser una de las especies con mayor distribución en México.

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BOOK NOTICE

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REFUGIO DE FITODIVERSIDAD EN LA CIUDAD DE MÉXICO, EL CASO DE LA CUENCA DEL RÍO MAGDALENA

V. Ávila-Akerberg, B. González-Hidalgo, M. Nava-López y L. Almeida-Leñero

Laboratorio de Ecosistemas de Montaña del
Departamento de Ecología y Recursos Naturales
Facultad de Ciencias, UNAM, MÉXICO, D.F.
Circuito exterior, Ciudad Universitaria, UNAM, C.P. 04510, MÉXICO
E-mail: vicaviak@gmail.com

RESUMEN

La cuenca del río Magdalena, reconocida por contener uno de los últimos ríos vivos en el Distrito Federal, registra una fitodiversidad de 87 familias con 251 géneros y 487 especies. Las familias más importantes por número de géneros y especies son: Asteraceae, Poaceae, Lamiaceae, Caryophyllaceae y Rosaceae. Los géneros con mayor número de especies son *Salvia* (13), *Ageratina* (10), *Pinus* (8) y *Quercus* (7). Se registraron diez especies incluidas en la NOM-059-SEMARNAT-2001, siendo tres además endémicas: *Acer negundo* var. *mexicanum*, *Furcraea bedinghausii*, *Dahlia scapigera* y como indicadoras de perturbación *Acaena elongata* y *Achillea millefolium*. La riqueza de plantas de esta área, abarca ca. del 25% de la diversidad florística de la cuenca del valle de México, o el 2.2% del total de la flora del país. Por esto, la cuenca del río Magdalena debe ser considerada un refugio para la conservación de la biodiversidad, ya que es la base para el mantenimiento de los servicios ecosistémicos más importantes de la zona.

Palabras Clave: Florística, fitodiversidad, cuenca del río Magdalena, México D.F.

ABSTRACT

The Magdalena River watershed, having one of the last living rivers of Mexico City, has a floristic diversity of 87 families, 251 genera, and 487 species. The most important plant families in terms of species and genera numbers are: Asteraceae, Poaceae, Lamiaceae, Caryophyllaceae, and Rosaceae. The genera with the most species are *Salvia* (13), *Ageratina* (10), *Pinus* (8), and *Quercus* (7). Ten plants included in the NOM-059-SEMARNAT-2001, the Mexican classification for endangered plant species, were recorded including three endemic species: *Acer negundo* var. *mexicanum*, *Furcraea bedinghausii*, *Dahlia scapigera*. Two species were recorded as disturbance indicators, *Acaena elongata* and *Achillea millefolium*. The plant species richness of this area represents ca. 25% of the total flora in the Valley of Mexico, and ca. 2.2% of the country's flora. Because of this, the Magdalena River watershed should be considered a conservation area of rich biodiversity. The watershed serves as the basis and the maintenance of the most important ecosystem services provided to the area.

INTRODUCCIÓN

México es un país megadiverso dada su ubicación dentro de las regiones Neártica y Neotropical (Rzedowski 1978). Su flora nativa oscila entre 75 órdenes, 304 familias, 2,804 géneros y 22,351 especies, en los 200 millones de ha de superficie que abarca el país (Villaseñor 2004). Este mismo autor, utilizó métodos no paramétricos para estimar la fitodiversidad total del país, así se añadirían a estas cifras más de 6,500 especies, por lo que la flora fanerogámica deberá estar en el orden de las 29,000 especies. Con estas cifras la República Mexicana ocupa el quinto lugar entre los países con mayor riqueza florística del mundo (Sarukhán & Dirzo 2001). Sin embargo, el conocimiento de su fitodiversidad es todavía incompleto (Villaseñor 2004).

La zona templada subhúmeda del territorio mexicano cubre la mayor parte de las áreas montañosas del país, con una superficie de ca. 33 millones de ha, que corresponde al 15% de la superficie nacional (Toledo & Ordoñez 1998). Esta zona se caracteriza por contener elementos holárticos, predominantemente en el estrato arbóreo, mientras que los estratos arbustivo y herbáceo son neotropicales, formando un complejo mosaico con los elementos autóctonos (Rzedowski 1978). Los principales tipos de vegetación en esta región son los bosques de coníferas, bosque mixto y bosque de *Quercus*, mientras que el bosque mesófilo de montaña, el cual pertenece a la zona templada húmeda, representa una transición entre las regiones tropicales y templadas (Rzedowski 1970). La flora de estos bosques de coníferas junto con la del bosque de *Quercus*, representan cerca de 25% del total de la flora vascular de México (ca. 7,000 especies), de las cuales ca. 4,900 especies son endémicas (Rzedowski 1991).

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La cuenca del Valle de México (CVM) contiene bosques de filiación templada en las que se desarrollan cerca del 2% de las plantas del planeta (Calderón de Rzedowski & Rzedowski 2001). En esta cuenca endorreica de origen volcánico con una extensión ca. de 7,500 km^2, se ubica el Distrito Federal que, a pesar de contener una de las ciudades más grandes del mundo, todavía cuenta con importantes áreas con vegetación natural, las cuales representan el 58% de su territorio (Corenader 2006).

Dentro del Distrito Federal, se encuentra la delegación política Magdalena Contreras, la cual ocupa el 9° sitio en extensión territorial, y más del 70% de su superficie corresponde a la categoría de suelo de conservación. Sin embargo, el conocimiento sobre la fitodiversidad es limitado.

En la Delegación Magdalena Contreras se localiza el río Magdalena, el cual representa uno de los cuerpos de agua más importantes del Distrito Federal (Delegación la Magdalena Contreras, 2006). El tipo de suelo y la cobertura forestal que ésta presenta, promueve la infiltración del agua de lluvia hacia los mantos acuíferos de la CVM (Mazari 2000), por lo que un excedente hídrico de 10% podría ser aprovechado en la zona urbana (Jujnovsky 2006). Al río Magdalena se le reconoce como un río vivo del Distrito Federal y existe un interés reciente por parte de las autoridades de la ciudad en manejar integralmente la cuenca.

Debido a que estos bosques enfrentan una gran presión antrópica, es importante conocer la fitodiversidad de estas comunidades boscosas, con la finalidad de evaluar su estado de conservación y poder proponer alternativas para su mantenimiento. Este trabajo presenta el inventario inicial de la fitodiversidad de plantas vasculares de la cuenca del río Magdalena (CRM) y su zona de influencia.

Antecedentes.—Algunos de los autores que han realizado estudios previos de florística y vegetación en la CRM y zonas adyacentes son: Rzedowski (1954) hizo un análisis de la fitodiversidad en el matorral xerófilo del pedregal de San Ángel, Madrigal (1967), estudió el bosque de *Abies religiosa* en las zonas montañosas de la CVM, Rzedowski (1970), realizó una descripción para el bosque mesófilo de montaña en la CVM, encontrando algunos fragmentos dentro de la CRM, Velázquez y Cleef (1993), definieron las asociaciones vegetales en los volcanes Tláloc y Pelado, y Nieto de Pascual (1995) describió la estructura y composición de los bosques de *Abies religiosa* en la CRM. En el 2001, Calderón de Rzedowski y Rzedowski actualizaron la información sobre la flora del valle de México, estimada en alrededor de 2500 especies, la cual ha sido base para estudios recientes como los de Ávila-Akerberg (2002) y Nava (2003), quienes presentan datos de cobertura de las especies registradas por comunidad vegetal, así como su relación con diversas variables ambientales en la CRM.

Área de estudio.—Localización física.– La cuenca del río Magdalena (CRM) se ubica dentro de la Cordillera Volcánica Transmexicana (CVT), en la provincia florística de las Serranías Meridionales, dentro de la región Mesoamericana de Montaña (Rzedowski 1978). Esta área forma parte de la CVM en la vertiente occidental de la sierra de las Cruces con un intervalo altitudinal de los 2,530 a los 3,870 msnm y una extensión aproximada de 3,000 ha (Fig. 1).

Relieve.—Los bosques de la CRM se desarrollan en un relieve montañoso, dada su ubicación dentro de la CVT. El modelado del paisaje se debe principalmente a la acción erosiva hídrica y a los procesos fisicoquímicos, siendo el desgaste de la corriente del río Magdalena el que ha ido formando un valle intermontano longitudinal joven (Álvarez 2000).

Geología.—El área de estudio presenta diferentes etapas en su evolución relacionada directamente con el origen de la CVM (Ontiveros 1980). Esta zona está formada por material ígneo extrusivo, producto de manifestaciones volcánicas del Terciario y Cuaternario (Álvarez 2000). El basamento de la CRM, está constituido por macizos de la sierra de las Cruces, de principios del Terciario, alcanzando el Terciario Superior. Esta sierra es uno de los principales focos de actividad del CVT que se formó como consecuencia de una serie de emisiones pacíficas de lavas ácidas. Formaciones posteriores, dan lugar a los cerros de San Miguel y la Palma (Cervantes 1969). La CRM, es el resultado de un afallamiento en bloques que deja bancos abruptos de forma regular en donde el río se encajona en márgenes estrechos (Álvarez 2000).

Hidrología.—El río Magdalena tiene un cauce de una longitud total de 21,600 m, de los cuales 15,200 m recorren los bosques de la cuenca del río Magdalena (Ávila-Akerberg 2004). Posteriormente, el río entra a

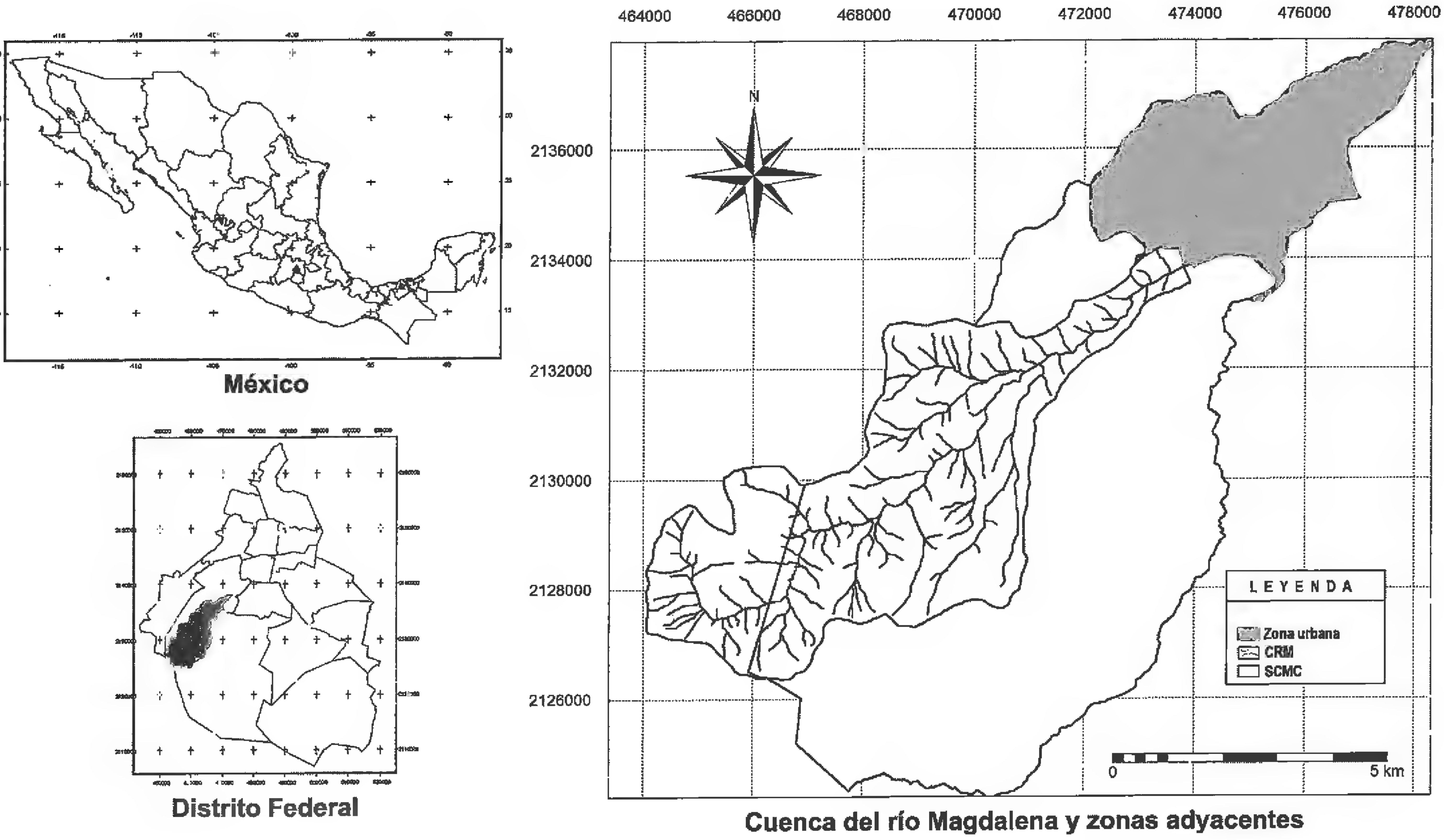

Fig. 1. Localización de la cuenca del río Magdalena y zonas de influencia con respecto a México y al Distrito Federal.

zona urbana hasta llegar a la presa Anzaldo en donde el río es entubado y dirigido hacia el río Churubusco. Las aguas continúan su recorrido para finalmente salir de la CVM a través de los túneles artificiales de Tequisquiac y llegar a la cuenca del río Tula (Álvarez 2000). Las características hidrológicas de la CRM se deben a factores como la altitud y la influencia de las masas marítimas, tanto del Golfo como del Pacífico, que favorecen las condiciones de humedad. Así mismo, la estructura geológica de la sierra de las Cruces y las precipitaciones han permitido que la zona mantenga una infiltración constante, generando una fuente de almacenamiento de agua (Ontiveros 1980).

Suelo.—El suelo en la CRM es resultado de una formación de material ígneo extrusivo, producto de manifestaciones volcánicas del Terciario y Cuaternario, predominando las Andesitas y Dacitas (Ontiveros 1980). Los suelos son, en su mayoría, Andosoles del tipo húmico, mólico, ócrico con mezcla de Litosoles, con textura franco, migajón arcilloso y arenoso. Los suelos con textura franca se encuentran distribuidos en toda la región. En las partes altas, el pH es más ácido y el contenido de materia orgánica es mayor (Jujnovsky 2006).

Clima.—En la parte baja de la CRM, entre los 2530 y 2800 msnm, se presenta el subtipo climático C (w_2) (w) (b) i'g (Köppen modificado por García 1987); templado subhúmedo, el más húmedo de los subhúmedos con régimen de lluvias de verano y porcentaje de lluvia invernal menor al 5%. El verano es fresco y largo, la temperatura media anual oscila entre 12 y 18° C, la temperatura del mes más frío entre -3 y 18° C y la del mes más caliente entre 6.5 y 22° C, con poca oscilación térmica y marcha de la temperatura tipo Ganges. En la parte alta, de los 2800 a los 3500 msnm el clima es Cb' (w_2) (w) (b') i g, difiriendo del anterior por tener una temperatura media anual entre 5 y 12° C con oscilación térmica menor a 5° C, es decir, isotermal (García 1987).

Los porcentajes de lluvia altos se registran para el período de mayo a octubre, siendo el mes de julio cuando se alcanza una precipitación que supera los 250 mm. Las mayores temperaturas acontecen desde marzo hasta octubre, siendo el mes de mayo el más caluroso y enero el más frío (Álvarez 2000).

Vegetación.—Los elementos físicos que componen al área de estudio, tales como el relieve montañoso, el sustrato rocoso -producto de evolución geológica-, el clima, la existencia de agua de manantiales y ríos, así

como los suelos, han permitido el desarrollo de la vegetación templada, donde se presentan gran variedad de especies de importancia biológica y económica.

De acuerdo a la clasificación de vegetación propuesta por Rzedowski (1978), la vegetación presente en la zona es principalmente de coníferas como: *Abies religiosa* y *Pinus hartwegii*. También se encuentran mezclas de estas especies de coníferas con otras latifoliadas como *Quercus* spp., conformando lo que se conoce como bosque mixto. En pequeños parches es posible encontrar bosque mesófilo de montaña, caracterizado por especies como: *Quercus* spp., *Garrya laurifolia, Clethra mexicana* y *Viburnum stenocalyx*, entre otras.

MÉTODO

La recolecta de ejemplares fue realizada durante las múltiples visitas a la zona de estudio entre 2004 y 2006, en 128 sitios de muestreo, dentro de los diferentes tipos de vegetación de la CRM y zonas adyacentes. En estos sitios se registraron datos ambientales de altitud, pendiente, orientación y suelo desnudo.

Los ejemplares fueron herborizados, etiquetados y determinados a nivel de especie con ayuda de claves taxonómicas especializadas para la zona (Beetle 1983 y 1987; Calderón de Rzedowski & Rzedowski 2001, Espinosa & Sarukhán 1997). Para las determinaciones botánicas se siguió la clasificación propuesta por Cronquist (1988) para dicotiledóneas y para monocotiledóneas la de Dahlgren et al. (1985). Las sinonimias y nomenclatura de los nombres científicos se corroboraron en la base de datos del Missouri Botanical Garden (www.mobot3.org). El material colectado fue depositado en la colección del Herbario FCME (Facultad de Ciencias, UNAM).

Se identificaron las especies arvenses y ruderales consultando los trabajos de Espinosa & Sarukhán (1997) y Calderón de Rzedowski & Rzedowski (2001). Se realizó un análisis de coeficiente de relación entre las especies y géneros de la familia Asteraceae contra el total de las especies para comprobar la intensidad de muestreo (Rzedowski 1991).

RESULTADOS

El estudio registró un total de 87 familias con 251 géneros y 487 especies en la lista florística (Apéndice 1). Las familias más importantes en cuanto al número de especies son: Asteraceae 21%, Poaceae 4.9%, Lamiaceae 4.7%, Caryophyllaceae 4.3, Rosaceae 3.7% y Brassicaceae 3.5% (Tabla 1), mientras que, las familias con mayor número de géneros son: Asteraceae 18.2%, Poaceae 5.7%, Brassicaceae 5.3%, Fabaceae 4.0%, Rosaceae 4.0% y Lamiaceae 2.8%. Los géneros con más especies son *Salvia* (13), *Ageratina* (10), *Pinus* (8), *Quercus* (7), y *Roldana* y *Senecio* con (6).

En cuanto a las formas de crecimiento (por especie, Fig. 2) las herbáceas son las más abundantes (365 especies), seguido de las arbóreas (49), arbustivas (44), rasantes (20), trepadoras (5) y epífitas (4).

Por forma de crecimiento a nivel de familias las más numerosas son: en hierbas Asteraceae con 79 especies, Poaceae con 24, Lamiaceae con 23, Caryophylaceae 18, Brassicaceae con 15 y Fabaceae y Cyperaceae con 12. Para los arbustos, Asteraceae con 20 especies, y Ericaceae y Rosaceae con 3 especies cada una; en el arbóreo, Pinaceae con 9, Fagaceae con 7 y Betulaceae con 4 (Fig. 3).

De la lista florística resultante (487 especies), se registraron 10 especies en alguna categoría de riesgo de acuerdo a la Norma Oficial Mexicana 059-SEMARNAT-2001 (DOF, 2002), de las cuales 3 son endémicas a México: *Furcraea bedinghausii, Acer negundo* var. *mexicanum* y *Dahlia scapigera* (Tabla 2). Otras especies, por el contrario, se ven favorecidas por condiciones de perturbación por lo que es común encontrarlas en cultivos (arvenses) o bien a la orilla de caminos (ruderales). Dentro de estas especies se encuentran: *Acaena elongata, Achillea millefolium, Ageratina petiolaris, Cerastium nutans, C. vulcanicum, Drymaria laxiflora, Erigeron galeottii, Geranium seemannii, Roldana angulifolia, Senecio cinerarioides* y *Sigesbeckia jorullensis*, entre otras. El total de las especies arvenses y/o ruderales fue de 69.

El valor de coeficiente especies-géneros (e/g) para la familia Asteraceae fue de 2.3, en tanto que el coeficiente e/g para el total de la flora registrada en este estudio fue de 1.94, dando una diferencia de 0.36.

TABLA 1. Familias de plantas vasculares mejor representadas en la CRM, México, D. F.

Familia	No. géneros	% géneros	No. especies	% especies
Asteraceae	45	18.2	102	21.0
Poaceae	14	5.7	24	4.9
Brassicaceae	13	5.3	17	3.5
Rosaceae	10	4.0	18	3.7
Fabaceae	10	4.0	17	3.5
Lamiaceae	7	2.8	23	4.7
Scrophulariaceae	6	2.4	10	2.1
Apiaceae	6	2.4	9	1.9
Solanaceae	5	2.0	15	3.1
Crassulaceae	5	2.0	11	2.3
Rubiaceae	5	2.0	9	1.9
Caryophyllaceae	4	1.6	21	4.3
Cyperaceae	4	1.6	12	2.5
Onagraceae	4	1.6	9	1.9
Polygalaceae	4	1.6	9	1.9
Ranunculaceae	3	1.2	8	1.6
Pinaceae	2	0.8	9	1.9
Fagaceae	1	0.4	7	1.4

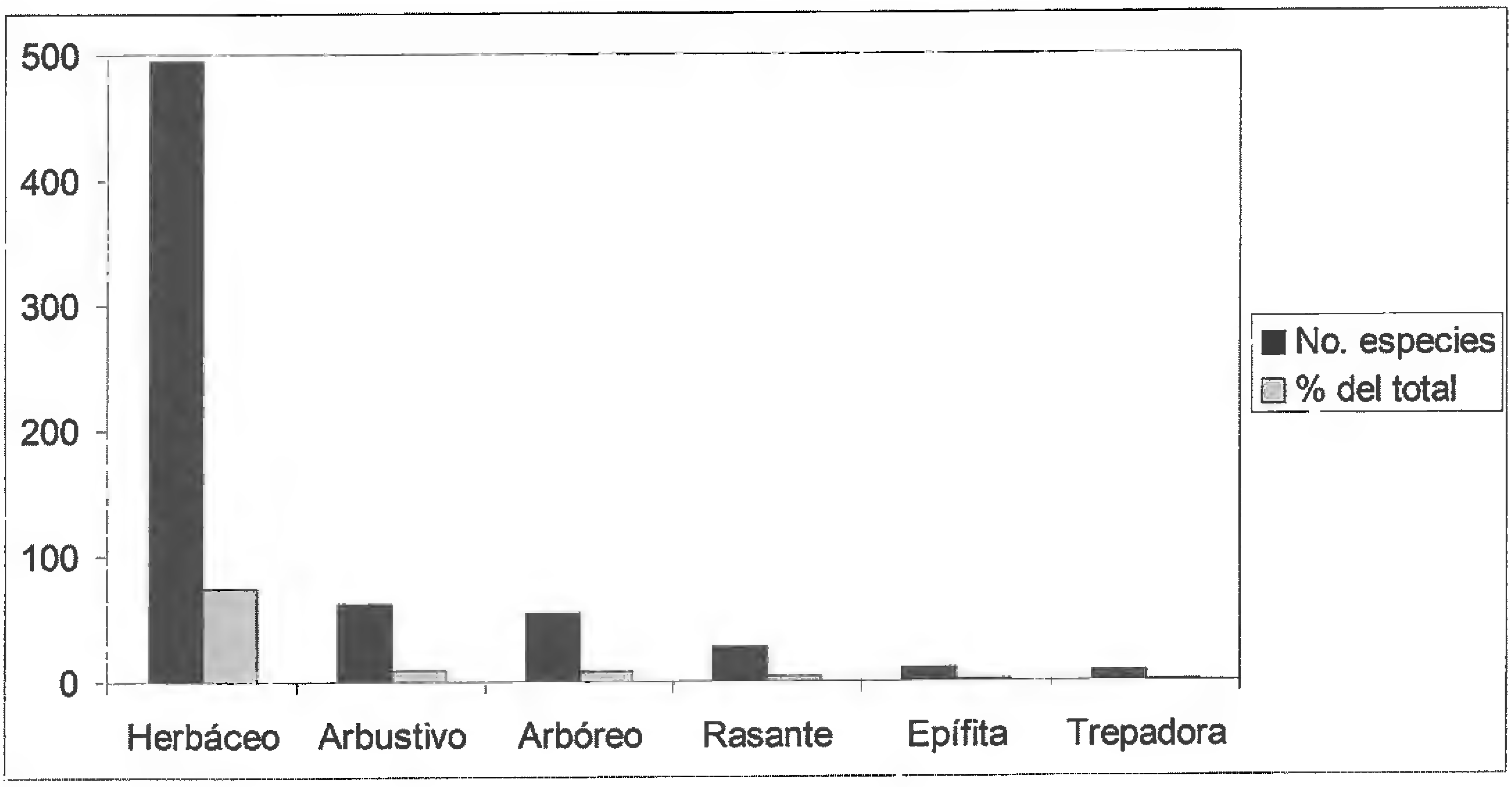

FIG. 2. Formas de crecimiento dominantes, en número y porcentaje en la CRM, México, D.F.

DISCUSIÓN

Los resultados de este estudio muestran que la CRM es una de las localidades más importantes como refugio de fitodiversidad dentro del suelo de conservación del Distrito Federal. En el área de estudio se encuentran todos los principales tipos de vegetación templados del país y la riqueza florística es mayor o similar a la encontrada en zonas cercanas (e.g., Cornejo-Tenorio et al. 2003; Castillo et al. 2004; Sánchez-González et al. 2005).

En cuanto al número de especies, las del estrato herbáceo dominan, lo que corresponde a lo obser-

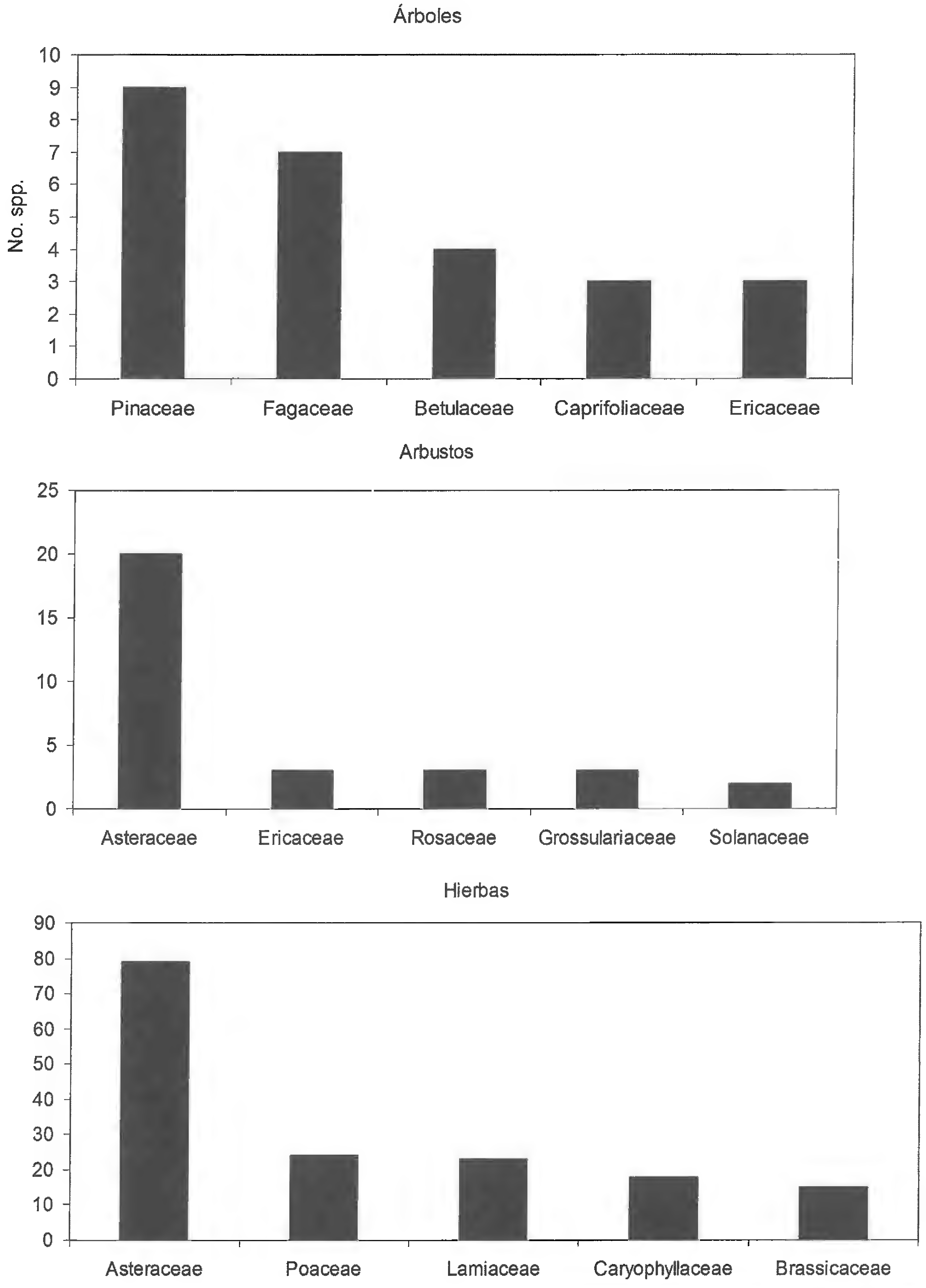

Fig. 3 Principales familias por formas de crecimiento en la CRM, México, D.F.

vado por Rzedowski (1978) y Cornejo-Tenorio *et al.* (2003) para la generalidad de los bosques templados de México. Sin embargo, considerando la cobertura, el estrato arbustivo es el dominante, lo que puede ser un indicador del deterioro de la zona. Este se explica por la deforestación, lo que genera claros en el dosel del estrato arbóreo permitiendo o estimulando el crecimiento de los arbustos.

El endemismo en las especies de la CRM, presenta proporciones similares a las evaluaciones previas de la flora de las regiones montañosas de México, ya que Rzedowski (1991) estima que la proporción de especies endémicas del país para los bosques de coníferas y de encino equivale al 70% y para el bosque mesófilo de montaña, a 30%.

La familia Asteraceae, con 102 especies, es la mejor representada en la cuenca, seguida en menor proporción por Poaceae, Lamiaceae, Rosaceae, Fabaceae y Brassicaceae. Este patrón de predominio florístico ha sido encontrado también en otros trabajos realizados en tipos de vegetación similares a los de la cuenca, como es el caso del Parque Nacional Lagunas de Zempoala (Bonilla y Viana-Lases, 1997), en el volcán Popocatépetl (Almeida-Leñero et al. 1997), el área de San Juan Nuevo Paranguricutiro (Medina-García et al. 2000) y la Reserva de la Biosfera de la Mariposa Monarca (Cornejo-Tenorio et al. 2003). Se ha visto que en las latitudes donde la familia de las compuestas juega un papel importante, el cociente entre el número de especies y géneros de compuestas se aproxima al mismo valor para toda la flora fanerogámica de un área. Para la cuenca del río Magdalena se encontró que este cociente es de 2.3, y si se multiplica por el número total de géneros (250) nos da 579 especies, número relativamente mayor al total de especies en el área de estudio (487 spp). Esto indica que algunas de estas especies han desaparecido, que hay sinonimias, inconsistencias en los listados o que aún es insuficiente el esfuerzo de colecta. Sin embargo, al revisar los trabajos realizados por autores como Reiche (1914), Madrigal (1967), Sánchez (1969), Rzedowski (1970), Nieto de Pascual (1995) y Calderón de Rzedowski y Rzedowski (2001), se cuantificó un mayor número de especies en la zona, que las registradas en este estudio. Por lo tanto, es fundamental continuar con el monitoreo de la flora en la zona, sirviendo éste como herramienta para medir el grado de conservación.

Los resultados que se presentan en este estudio muestran el papel fundamental que desempeña la CRM como área de conservación de la flora mexicana, no sólo por la riqueza florística sino también por la cantidad de especies endémicas (ca. 85 especies) y en alguna categoría de protección. La Delegación Magdalena Contreras presenta más del 78% de su territorio como suelo de conservación, por lo tanto la riqueza de especies en esa superficie es relevante si consideramos que por ejemplo, en el caso de plantas, se alberga poco más del 25% de la diversidad florística que existe en el valle de México o el 2.2% de la riqueza total del país. Si además se toma en cuenta la presencia en la zona de uno de los últimos ríos vivos en el Distrito Federal y la presencia de elementos del bosque mesófilo de montaña casi desaparecidos de la CVM, es fundamental priorizar el cuidado y recuperación de esta cuenca.

Se espera que la información florística proporcionada por la presente contribución pueda ser útil en la elaboración del plan de manejo integral de la zona, que representa un refugio de esta fitodiversidad y que juega un papel importante en el mantenimiento de numerosos servicios ecosistémicos que brinda a la ciudad. A partir de esta información, es importante fomentar estudios similares en zonas adyacentes abordando además otros aspectos biológicos, sociales, económicos y políticos.

APÉNDICE 1

PLANTAS NO VASCULARES

Bryophyta

Grimmiaceae
Grimmia tolucensis Card.—Rastrera, VA-168

Pottiaceae
Trichostomum cylindricum (Bruch.) C.M.—Rastrera, JB-8

Thuidiaceae
Thuidium delicatulum (Herdw) Mitt.—Rastrera, BGH-2968

PLANTAS VASCULARES

Equisetophyta

Equisetaceae
Equisetum hyemale L. ssp. *affine* (Engelm.) Calder & Roy L. Taylor—Hierba, VA-147

Pteridopsida

Adiantaceae
Adiantum ampillus-veneris L.—Hierba, VA-2

Adiantum andicola Liebm.—Hierba, VA-3
Adiantum marginatum Bory—Hierba, MV-1

Aspleniaceae
Asplenium monanthes L.—Hierba, VA-16

Dryopteridaceae
Cystopteris fragilis (L.) Bernh.—Hierba, JB-4
Dryopteris parallelogramma (Kunze) Alston—Hierba, JB-5
Plecosorus speciossisimus (A. Braun ex Kunze) T. Moore—Arbusto, VA-145
Polystichum rachichlaena Fée—Hierba, VA-146

Polypodiaceae
Cheilanthes farinosa (Forssk.) Kaulf.—Hierba, JB-6
Cheilanthes hirsuta Link.—Rastrera, JB-7
Cheilanthes marginata Kunth.—Hierba, VA-266
Cheilanthes sinuata (Lag. ex Sw.) Domin—Hierba, VA-267

Pteridaceae
Pteridium aquilinum (L.) Kuhn—Hierba, VA-271

Coniferophyta

Cupressaceae
Cupressus lusitanica Mill.—Árbol, MR-22

Pinaceae
Abies religiosa (Kunth) Schltdl. & Cham.—Árbol, VA-230
Pinus ayacahuite C. Ehrenb. ex Schltdl. var. *veitchii* (Roezl) Shaw—Árbol, VA-231
Pinus hartwegii Lindl.—Árbol, VA-232
Pinus leiophylla Schiede ex Schltdl.—Árbol, VA-233
Pinus montezumae Lamb.—Árbol, VA-234
Pinus patula Schltdl. & Cham.—Árbol, VA-235
Pinus pseudostrobus Lindl.—Árbol, VA-236
Pinus rudis Endl.—Árbol, VA-237
Pinus teocote Schltdl. & Cham.—Árbol, VA-238

Magnoliophyta

Aceraceae
Acer negundo L.var. *mexicanum* (DC.) Standl. & Roy L. Taylor—Árbol, VA-1

Amaranthaceae
Iresine ajuscana Suessenguth & Beyerle—Hierba, BGH-2977
Iresine diffusa Humb. & Bompl—Hierba, BGH-2978
Iresine elongata Humb. & Bompl. ex Willd.—Hierba, VA-7

Amaryllidaceae
Zephyranthes carinata (Lindl.) Benth.—Hierba, VA-8
Zephyranthes fosteri Traub.—Hierba, VA-9

Apiaceae
Arracacia atropurpurea (Lehm.) Benth. & Hook ex Hemsl.—Hierba, VA-10
Daucus montanus Humb. & Bonpl. ex Spreng.—Hierba, VA-11
Donnellsmithia juncea (Humb. & Bonpl.) Mathias & Constance—Hierba, VA-12
Eryngium carlinae F. Delaroche—Hierba, VA-13
Eryngium proteaeflorum F. Delaroche—Hierba, MR-1
Eryngium serratum Cav.—Hierba, MV-4
Eryngium subacaule Cav.—Hierba, MR-2
Osmorhiza mexicana Griseb.—Hierba, VA-14
Tauschia alpina (J. C. Coult. & Rose) Mathias—Hierba, VA-15

Asclepiadaceae
Asclepias ovata M. Martens & Galeotti—Hierba, MV-5
Matelea pedunculata (Decasine) Woodson—Hierba, JB-1

Asteraceae
Achillea millefolium L.—Hierba, ruderal, VA-17
Ageratina enixa (Rob.) R.M. King & H. Rob.—Hierba, VA-18
Ageratina glabrata (Kunth) R.M. King & H. Rob.—Arbusto, VA-19
Ageratina mairetiana (DC.)R.M. King & H. Rob.—Arbusto, VA-20
Ageratina oligocephala (DC.)R.M. King & H. Rob.—Hierba, VA-21
Ageratina pazcuarensis (Kunth) R.M. King & H. Rob.—Hierba, VA-22
Ageratina petiolaris King. & H. Rob.—Hierba, ruderal, MV-6
Ageratina prunellifolia (Kunth) R.M. King & H. Rob.—Hierba, MV-7
Ageratina rhomboidea (Kunth) R.M. King & H. Rob.—Arbusto, MV-8
Ageratina rivalis (Greenm.) R.M. King & H. Rob.—Arbusto, MV-9
Ageratina vernicosa (Sch. Bip. ex Greenm.) R.M. King & H. Rob.—Arbusto, VA-23
Ageratum corymbosum Zucc. ex Pers—Arbusto, VA-24
Archibaccharis asperifolia (Benth.) S.F. Blake—Arbusto, VA-25
Archibaccharis hieracioides (S.F. Blake) S.F. Blake—Hierba, MR-3
Archibaccharis hirtella (DC.) Heering—Trepadora, MR-4
Archibaccharis schiedeana (Benth. in Oerst.) J.D. Jackson.—Hierba, MR-5
Archibaccharis serratifolia (Kunth) Blake—Hierba, VA-26
Artemisia ludoviciana Nutt. ssp. *mexicana* (Willd. Ex Spreng.) D.D. Keck—Hierba, arvense y ruderal, MV-10
Aster subulatus Michx.—Hierba, arvense, VA-27
Baccharis conferta Kunth—Arbusto, VA-28
Baccharis multiflora Kunth—Hierba, VA-29
Bidens anthemoides (DC.) Sherff—Hierba, arvense, MR-6
Bidens aurea (Aiton) Sherff—Hierba, MR-7
Bidens odorata Cav.—Hierba, arvense, MV-11
Bidens ostruthioides (DC.) Sch. Bip.—Hierba, MV-12
Bidens serrulata (Poir.) Desf.—Hierba, arvense, MV-13
Bidens triplinervia Kunth—Hierba, VA-30
Brickellia nutanticeps S.F. Blake—Hierba, MR-8
Brickellia pendula (Schrad.) A. Gray—Hierba, MR-9
Brickellia scoparia (DC.) A. Gray—Hierba, VA-31
Cirsium ehrenbergii Sch. Bip.—Hierba, VA-32
Cirsium jorullense (Kunth) Spreng. ssp. *jorullense*—Hierba, VA-33
Cirsium nivale (Kunth) Sch. Bip.—Hierba, VA-34
Conyza schiedeana (Less.) Cronquist—Hierba, VA-35
Cosmos bipinnatus Cav.—Hierba, arvense, VA-36
Dahlia coccinea Cav.—Hierba, MV-14
Dahlia scapigera (A. Dietr.) Knowles & Westc.—Hierba, VA-37
Erigeron galeottii (A. Gray) Greene—Hierba, ruderal, VA-38
Erigeron karvinskianus DC.—Hierba, VA-39

Erigeron longipes DC.—Hierba, VA-40
Erigeron pubescens Kunth—Hierba, VA-41
Eupatorium lucida (Ortega) R.M. King & H. Rob.—Arbusto, VA-42
Eupatorium oreithales (Greenm.) B.L. Turner.—Hierba, VA-43
Eupatorium schaffneri Sch. Bip. ex Robinson—Arbusto, MV-15
Florestina pedata (Cav.) Cass.—Hierba, arvense, VA-44
Galinsoga parviflora Cav.—Hierba, arvense, MR-10
Gamochaeta americana (Mill.) Wedd.—Hierba, arvense, VA-45
Gnaphalium chartaceum Greenm.—Hierba, arvense y ruderal, VA-46
Gnaphalium inornatum DC.—Hierba, VA-47
Gnaphalium liebmanii Sch. Bip. ex Klat. var. *monticola* (McVaugh) D.L. Nash.—Hierba, MR-11
Gnaphalium salicifolium (Bertol.) Sch. Bip.—Hierba, MR-12
Gnaphalium semiamplexicaule DC.—Hierba, arvense, VA-48
Haplopappus stoloniferus DC.—Hierba, VA-49
Helenium scorzoneraefolium (DC.) A. Gray—Hierba, MR-13
Helianthus lacinata A. Gray—Hierba, MV-16
Hieracium dysonymum S.F. Blake—Hierba, MV-17
Hieracium mexicanum Less.—Hierba, MV-18
Hymenostephium microcephalum (Lees.) S.F. Blake—Rastrera, MR-14
Melampodium repens Sessé & Moc.—Hierba, VA-50
Montanoa frutescens (Mairet. ex DC.) Hemsl.—Arbusto, VA-51
Oxylobus adscendens (Sch. Bip. ex Hemsl.) R. L. Rob & Greenm.—Hierba, VA-52
Oxylobus arbutifolius (Kunth) A. Gray—Hierba, VA-53
Packera sanguisorbae (DC.) C. Jeffrey—Hierba, VA-54
Packera toluccana (DC.) W.A. Weber & Á. Löve—Hierba, VA-55
Parthenium hysterophorus L.—Hierba, MV-19
Perymenium berlandieri DC.—Arbusto, VA-56
Pinaropappus (Less.) Less. var. *roseus*—Hierba, VA-57
Piqueria pilosa Kunth—Hierba, VA-58
Piqueria trinervia Cav.—Hierba, MR-15
Pseudognaphalium arizonicum A. Gray—Hierba, MR-16
Pseudognaphalium oxyphyllum DC.—Hierba, MR-17
Pseudognaphalium oxyphyllum DC. var. *nataliae* F.J. Espinosa—Hierba, VA-59
Roldana albonervia (Greenm.) H. Rob. & Brettell—Arbusto, VA-60
Roldana angulifolia (DC.) H. Rob. & Brettell—Arbusto, VA-61
Roldana barba-johannis (DC.) H. Rob. & Brettell—Arbusto, VA-62
Roldana platanifolia (Benth.) H. Rob. & Brettell—Hierba, VA-63
Roldana reticulata (DC.) H. Rob. & Brettell—Hierba, MV-20
Roldana sinuata B.L. Turner—Hierba, VA-64
Sabazia humilis (Kunth) Cass.—Hierba, arvense, VA-65
Sanvitalia procumbens Lam.—Rastrera, arvense, VA-66
Senecio callosus Sch. Bip.—Hierba, VA-67
Senecio cinerarioides Kunth—Arbusto, indicadora de incendios, VA-68
Senecio jacalensis Greenm.—Hierba, VA-69
Senecio multidentatus Sch. Bip. ex Hemls.—Hierba, VA-70
Senecio roseus Sch. Bip.—Hierba, MV-21
Senecio salignus DC.—Arbusto, VA-71
Sigesbeckia jorullensis Kunth—Hierba, arvense, MV-22
Sigesbeckia orientalis L.—Hierba, VA-72
Sonchus oleraceus L.—Hierba, VA-73
Stevia glandulosa Hook. & Arn.—Hierba, VA-74
Stevia incognita Grashoff—Hierba, MV-23
Stevia monardifolia Kunth—Hierba, MV-24
Stevia myricoides McVaugh—Hierba, MV-25
Stevia ovata Willd. var. *ovata*.—Hierba, MV-26
Stevia purpusii B.L. Rob.—Hierba, VA-75
Tagetes erecta L.—Hierba, VA-76
Tagetes triradiata Greenm.—Hierba, VA-77
Taraxacum officinale L.—Hierba, arvense y ruderalVA-78
Verbesina oncophora B.L. Rob. & Seaton—Arbusto, MV-27
Verbesina virgata Cav.—Arbusto, VA-79
Vernonia alamanii DC.—Arbusto, VA-80
Villanova achillaeoides (Less.) Less.—Hierba, VA-81

Berberidaceae

Berberis moranensis Schult. & Schult. f.—Árbol, VA-82
Berberis schiedeana Schltdl.—Arbusto, VA-83

Betulaceae

Alnus acuminata Kunth ssp. *arguta* (Schltdl.) Furlow—Árbol, VA-84
Alnus acuminata Kunth ssp. *glabrata* (Fernald.) Furlow—Árbol, VA-85
Alnus jorullensis Benth. ssp. *jorullensis*—Árbol, VA-86
Alnus jorullensis Benth. ssp. *lutea* J.J. Furlow—Árbol, VA-87

Boraginaceae

Hackelia mexicana (Schltdl. & Cham.) I.M. Johnst.—Hierba, MV-28
Lasiarrhenum trinervium (Lehm.) B.L. Turner—Hierba, VA-88
Lithospermum strictum Lehm.—Hierba, ruderal, VA-89
Myosotis sylvatica Hoffm.—Hierba, MV-29

Brassicaceae

Barbarea orthoceras Ledeb.—Hierba, VA-90
Brassica campestris L.—Hierba, VA-91
Brassica rapa L.—Hierba, MV-30
Capsella bursa-pastoris L. Medic—Hierba, VA-92
Cardamine hirsuta L.—Hierba, MN-1
Cardamine obliqua Hochst.—Hierba, VA-93
Descurainia impatiens (Cham. & Schltdl.) O.E. Schultz—Hierba, arvense, VA-94
Draba jorullensis Kunth—Hierba, VA-95
Draba nivicola Rose—Hierba, VA-96
Eruca sativa Mill.—Hierba, arvense, MV-31
Erysimum capitatum (Douglas ex Hook.) Greene—Hierba, MV-32
Lepidium virginicum L. var. *pubescens* (Greene) C.L. Hitchc.—Hierba, arvense, MV-33
Pennellia longifolia (Benth.) Rollins—Hierba, VA-97
Raphanus raphanistrum L.—Hierba, arvense, VA-99
Rorippa mexicana (Moc. & Sessé) Standl. & Steyermark—Hierba, VA-98

Rorippa nasturtium-aquaticum (L.) Hayek—Rastrera, MR-18
Sisymbrium officinalis (L.) Scop—Rastrera, VA-100

Buddlejaceae
Buddleja cordata Kunth ssp. *cordata* Kunth—Árbol, VA-102
Buddleja parviflora Kunth—Árbol, MV-34

Campanulaceae
Diastatea micrantha (Kunth) McVaugh—Hierba, ruderal, MV-35
Diastatea tenera (A. Gray) McVaugh—Hierba, VA-103
Lobelia gruina Cav. var. *gruina*—Hierba, arvense y ruderal, VA-104
Lobelia laxiflora Kunth var. *angustifolia* A. DC.—Hierba, arvense y ruderal, VA-105
Lobelia schmitzii E. Wimmer—Hierba, VA-106

Caprifoliaceae
Sambucus nigra ver. *canadensis* L. (L.) B.L. Turner—Árbol, VA-107
Symphoricarpos microphyllus Kunth—Arbusto, VA-108
Viburnum stenocalyx (Oerst.) Hemsl.—Árbol, VA-109

Caryophyllaceae
Arenaria bourgaei Hemsl.—Rastrera, VA-110
Arenaria lanuginosa (Michx.) Rohrb.—Hierba, VA-111
Arenaria lycopodioides Willd. ex Schltdl.—Hierba, VA-112
Arenaria oresbia Greenm.—Hierba, VA-113
Arenaria paludicola Robins—Hierba, VA-114
Arenaria reptans Hemsl.—Rastrera, VA-115
Cerastium molle Bartl.—Hierba, VA-116
Cerastium nutans Raf.—Hierba, arvense, VA-117
Cerastium orithales Schltdl.—Hierba, VA-118
Cerastium purpusii Greenm.—Hierba, VA-119
Cerastium tolucense D.A. Good—Hierba, MR-19
Cerastium vulcanicum Schltdl.—Hierba, ruderal, VA-120
Drymaria effusa A. Gray—Hierba, VA-121
Drymaria laxiflora Benth.—Hierba, MR-20
Drymaria leptophylla (Cham. & Schltdl.) Fenzl ex Rohrb.—Rastrera, MR-21
Drymaria molluginea (Ser.) Didr.—Hierba, MV-36
Drymaria tenuis S. Watson—Hierba, MV-37
Drymaria villosa Schltdl. & Cham.—Hierba, ruderal, VA-122
Stellaria cuspidata Willd. ex Schltdl.—Hierba, VA-123
Stellaria media L.—Hierba, VA-124
Stellaria umbellata Turcz.—Hierba, MV-38

Cistaceae
Helianthemum glomeratum (Lag.) Lag. ex DC.—Hierba, VA-125

Clethraceae
Clethra mexicana DC.—Árbol, VA-127

Cornaceae
Cornus disciflora DC.—Árbol, VA-131
Cornus excelsa Kunth—Árbol, VA-132

Crassulaceae
Altamiranoa mexicana (Schltdl.) Rose—Hierba, VA-133
Echeveria gibbiflora Moc. & Sessé ex DC.—Hierba, VA-134
Echeveria secunda Booth ex Lindl.—Hierba, VA-135
Sedum batallae Barocio—Hierba, VA-136
Sedum bourgaei Hemsl.—Hierba, VA-137
Sedum jaliscanum S. Watson—Hierba, MV-41
Sedum moranense Kunth—Hierba, MV-42
Sedum oxypetalum Kunth—Arbusto, VA-138
Sedum praealtum A. DC. ssp. *parviflorum* (R.T. Clausen) R.T. Clausen—Hierba, VA-139
Tillaea connata Ruiz & Pavón—Hierba, VA-140
Villadia batessii Baehni & Macbride—Hierba, VA-141

Cucurbitaceae
Cucurbita radicans Naudin—Hierba, VA-142
Sicyos deppei G. Don—Hierba, arvense, VA-143
Sicyos parviflorus Willd.—Hierba, ruderal, VA-144

Ericaceae
Arbutus xalapensis Kunth—Árbol, VA-148
Chimaphila umbellata L.—Arbusto, MV-43
Comarostaphylis discolor (Hook.) Diggs var. *discolor*—Árbol, VA-149
Gaultheria lancifolia Small—Arbusto, VA-150
Vaccinium caepitosum Michx.—Arbusto, VA-151

Euphorbiaceae
Euphorbia furcillata Kunth var. *furcillata*—Hierba, VA-152
Euphorbia indivisa (Engelm.) Tidestr.—Hierba, MV-44
Euphorbia peplus L.—Hierba, VA-153
Euphorbia prostrata Ait.—Hierba, VA-154

Fabaceae
Acacia melanoxylon R. Br.—Árbol, VA-193
Astragalus guatemalensis Hemsl. var. *brevidentatus* (Hemsl.) Barneby—Hierba, VA-194
Dalea leporina (Ait.) Bullock—Hierba, MV-62
Desmodium aparines (Link) DC.—Hierba, MV-63
Desmodium molliculum (Kunth) DC.—Hierba, VA-195
Desmodium neomexicanum A. Gray—Hierba, VA-196
Erythrina coralloides DC.—Árbol, BGH-2983
Eysenhardtia polystachya (Ortega) Sarg.—Árbol, VA-197
Lathyrus odoratus L.—Hierba, VA-198
Lupinus elegans Kunth—Hierba, VA-199
Lupinus glabratus J. Agardh—Hierba, BGH-2984
Lupinus montanus Kunth—Hierba, VA-200
Senna multiglandulosa (Jacq.) H. S. Irwin & Barneby—Arbusto, BGH-2985
Trifolium amabile Kunth—Hierba, VA-201
Trifolium repens L.—Hierba, VA-202
Vicia faba L.—Hierba, BGH-2986
Vicia pulchella Kunth (Hemsl.) ssp. *mexicana* C.R. Gunn—Trepadora, BGH-2987
Vicia sativa L.—Trepadora, VA-203

Fagaceae
Quercus candicans Neé—Árbol, VA-155
Quercus castanea Neé—Árbol, VA-156
Quercus crassipes Humb. & Bonpl.—Árbol, VA-157
Quercus dysophylla Benth.—Árbol, VA-158
Quercus laurina Bonpl.—Árbol, MV-45
Quercus obtusata (Willd.) Pursh—Árbol, VA-159
Quercus rugosa Neé—Árbol, VA-160

Garryaceae
Garrya laurifolia Hartw. ex Benth. ssp. *laurifolia*—Árbol, MV-46

Gentianaceae
Gentiana ovatiloba (G. Don) Briq.—Hierba, VA-161
Gentianella quitense (Benth.) Gillett.—Hierba, VA-162
Halenia brevicornis (Kunth) G. Don—Hierba, VA-163
Halenia pringlei B.L. Rob & Seaton—Hierba, VA-164

Geraniaceae
Erodium cicutarium (L.) L´Hér. ex Aiton—Hierba, arvense, VA-165
Geranium latum Small—Hierba, MV-47
Geranium lilacinum Knuth—Hierba, MV-48
Geranium potentillaefolium DC.—Hierba, arvense, VA-166
Geranium seemanii Peyr.—Rastrera, arvense, VA-167

Grossulariaceae
Ribes affine Kunth—Arbusto, VA-169
Ribes ciliatum Humb. & Bonpl. ex Schult.—Arbusto, MR-33
Ribes coliosum Howell—Arbusto, MV-49

Guttiferae
Hypericum silenoides Juss. var. *mexicanum* (Keller) Rodr.—Hierba, VA-170

Hydrophyllaceae
Nama dichotomum Choisy var. *dichotomum* (Ruiz & Pav.) Choisy—Hierba, arvense, MV-50
Phacelia platycarpa (Cav.) Spreng.—Hierba, arvense, MV-51
Wigandia urens (Ruiz & Pav.) Kunth—Arbusto, ruderal, VA-171

Lamiaceae
Agastache mexicana (Kunth) Linton & Epling—Hierba, MV-56
Cunila lythrifolia Benth.—Hierba, VA-177
Lamium purpureum L.—Hierba, VA-178
Lepechinia caulescens (Ortega) Epling—Hierba, arvense, VA-179
Prunella vulgaris L.—Hierba, VA-180
Salvia amarissima Ortega—Hierba, VA-181
Salvia concolor Lamb.—Hierba, VA-182
Salvia elegans Vahl ex Benth.—Hierba, VA-183
Salvia gesneraeflora Lindl. & Paxton—Hierba, VA-184
Salvia mexicana L. var. *minor* (L.) Benth.—Hierba, VA-185
Salvia mexicana L.—Hierba, VA-186
Salvia microphylla L.var. *microphylla* L.—Hierba, VA-187
Salvia microphylla L.var. *neurepia* (Fern.) Epling—Hierba, VA-188
Salvia patens Cav.—Hierba, MV-57
Salvia polystachya Cav.—Hierba, MV-58
Salvia prunelloides Kunth.—Hierba, MV-59
Salvia reptans Jacq.—Hierba, VA-189
Salvia stricta Sessé & Moc.—Hierba, VA-190
Stachys agraria Schltdl. & Cham.—Hierba, arvense, VA-191
Stachys coccinea Ortega—Hierba, VA-192
Stachys eriantha Benth.–-Hierba, BGH-2979
Stachys repens M. Martens & Galeotti—Hierba, BGH-2980
Stachys sanchezii Rzed. & A. García—Hierba, VA 333

Lauraceae
Litsea glaucescens Kunth—Árbol, MR-34

Lentibulariaceae
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PRAXELIS CLEMATIDEA (ASTERACEAE), A GENUS AND SPECIES NEW FOR THE FLORA OF NORTH AMERICA

J. Richard Abbott

Department of Botany
University of Florida
Gainesville, Florida 32611, U.S.A.
Gainesville, Florida 32611, U.S.A.
jrabbott@botany.ufl.edu
and University of Florida Herbarium (FLAS)
Florida Museum of Natural History
379 Dickinson Hall, P.O. Box 110575
Gainesville, Florida 32611, U.S.A

C. LeAnn White

Department of Infectious Diseases
and Pathology
University of Florida
Gainesville, Florida 32611, U.S.A
WhiteC@vetmed.ufl.edu

S. Barry Davis

University of Florida Herbarium (FLAS)
Florida Museum of Natural History
379 Dickinson Hall, P.O. Box 110575
Gainesville, Florida 32611, U.S.A
taxon@flmnh.ufl.edu

ABSTRACT

Praxelis clematidea (Asteraceae) is a new genus and species for North America. *Praxelis* is compared with similar species, and their diagnostic characters are discussed.

RESUMEN

Praxelis clematidea (Asteraceae) es un género y especie nueva para América del Norte. Se compara *Praxelis* con especies parecidas, y se discuten sus caracteres diagnósticos.

Field work in central Florida by the second author has led to the discovery of a plant species new to North America, *Praxelis clematidea* (Griseb.) R.M. King & H. Rob. (Fig. 1). The species is native to Argentina, Bolivia, Paraguay, and Brazil (King & Robinson 1987). It is also erroneously reported from Venezuela (Waterhouse et al. 2003). It has been naturalized in Australia, China, and Hong Kong (Corlett & Shaw 1995; Veldkamp 1999; Waterhouse 2003). There are 13 additional species of *Praxelis* Cass., all restricted to South America, none of which are known as exotics elsewhere (King & Robinson 1987). A more complete description of *P. clematidea* is available on-line (U.S. Forest Service 2007), as are photos (Waterhouse et al. 2003), including comparison with the similar *Ageratum houstonianum* Mill. (Pollock et al. 2004).

Voucher specimen data: **UNITED STATES. Florida. Orange Co.:** 28°24'80"N 81°37'13"W (WGS84), NW of Kissimmee, on private property near the junction of Seidel Road with FL 429, abandoned ex-citrus grove (no citrus trees), herb ca. 2' tall, flowers pale purple, rare, 26 Jul 2006, *LeAnn White 1* [FLAS], det: S. Barry Davis (FLAS), Oct 2006, ver: John Pruski (MO), Mar 2007. **Orange Co.:** 28°24'9.7"N 81°37'11.5"W (WGS84), WSW of Orlando, SSW of Reedy Lake, near the Rapid Infiltration Basin Systems of the Reedy Creek Improvement District along Old Hartzog Road (gated), E of FL 429 and Bear Bay, W of Reedy Creek, accessed S off Seidel Road. Roadside and edge of pine plantation with *Bidens alba*, *Heterotheca subaxillaris*, *Lantana camara*, *Panicum maximum*, *Paspalum notatum*, and *Rhynchelytrum repens*, suffrutescent herb to ca. 1.3 m tall, usually with several branches from the base, with very strong smell (musky, cat-spray like), flowers pale pinkish purple, locally abundant, forming a large patch with hundreds of stems, 17 Jul 2007, *J. Richard Abbott 22887, with Tim Burns & Melissa Clark* [B, FLAS, G, GH, HBG, IJ, K, L, LD, M, MAD, MAPR, MEXU, MICH, MIN, MO, MSC, MT, MU, NY, PH, S, TEX, U, US, USCH, WU, Z]. **Orange Co.:** 28°26'56.9"N 81°35'46.6"W (WGS84), SW of Orlando, SE of Lake Hancock, NW corner of Lake Hancock Road at junction with Reams Road to S and Ficquette Road to N, accessed E of FL 429 on Seidel Road, which then turns N & E and becomes Lake Hancock Road. Roadside with *Bidens alba*, *Cyperus rotundus*, *Eupatorium capillifolium*, *Heterotheca subaxillaris*, *Paspalum notatum*, *Sida rhombifolia*, and *Urena lobata*, forming a large patch with ca. 50 plants here, 17 Jul 2007, *J. Richard Abbott 22888,*

with Melissa Clark [BM, BRIT, C, CAS, CICY, CONN, DAV, DUKE, E, EIU, F, FLAS, FSU, FTG, GOET, JBSD, LSU, MO, PIHG, SEL, UC, GA, UPRRP, USF, UWFP, W] and 8 Mar 2008, *J. Richard Abbott 24194* [FLAS]..

Praxelis clematidea: herb to suffrutescent shrub to ca. 1.3 m tall; stems soft pubescent (densely villous to hirsute, especially above); petioles usually very short, well less than 1/4 the blade length (except on the lowest leaves which may have petioles up to ca. 1/3 or more the blade length; these leaves are often gone by the time the plant is in fruit); blades ovate, rounded to cuneately narrowing at the base, generally about half (or more) as wide as long; margins irregularly toothed, i.e., some teeth nearly dentate, others more sharply serrate, with size variation even on same leaf; heads cylindrical-campanulate, clearly longer than wide (ca. 3–4 mm wide, 6–8 mm tall), in lax to dense clusters; phyllaries about 1 mm wide, flat, densely imbricate, although deciduous in fruit, with conspicuous dark striations from the veins.

A visit to the region on 17 July 2007 discovered hundreds of individuals of *Praxelis* at several scattered localities, all disturbed roadsides. This local abundance in so many different spots, in conjunction with the original collection in a relatively remote and inaccessible area, suggests that *Praxelis* has been in Florida for some time and has been spreading. The site where the species was first found in July 2006 is an open old field dominated by exotics [*Rhynchelytrum repens* (Willd.) C.E. Hubb.; *Richardia brasiliensis* Gomes; on edges, *Urena lobata* L.] and 'weedy' natives [*Cenchrus spinifex* Cav., *Heterotheca subaxillaris* (Lam.) Britton & Rusby, *Bidens alba* (L.) DC.]. The site is a dry, well-drained sandy upland that was once a citrus grove. Although there are no indisputable indicators of the original vegetation, sparse remnants suggest that it may have been sandhill vegetation, e.g., *Commelina erecta* L., *Croton glandulosus* L., *Galactia elliottii* Nutt., *Opuntia humifusa* (Raf.) Raf., *Passiflora incarnata* L., *Quercus myrtifolia* Willd. (only 1 plant seen), and, along the edges, *Euthamia caroliniana* (L.) Greene ex Porter & Britton and *Verbesina virginica* L. The area is now mostly surrounded by dry pine woods that appear secondary, with a remnant swampy baygall nearby to the southwest. The site has about 200 Florida gopher tortoises (*Gopherus polyphemus*) and a density of about 29.1 tortoises/ha, which is very dense for gopher tortoise populations. *Praxelis* was completely absent on a follow-up trip on 5 November 2006, at which time the site was also seen to be heavily disturbed by hog rooting (*Sus scrofa*). One small patch was rediscovered in the same area during a follow-up visit on 23 August 2007, making it clear that the species is established at the site. A follow-up trip on 8 March 2008 to the Lake Hancock Road site found that, as part of a road construction project, the population had been nearly eradicated (although achenes are doubtless still persisting in the area); only one plant was seen (and it was in flower), with the remaining area covered in fresh sod. This did demonstrate that at least some individuals of *Praxelis* over-winter as above-ground perennials, flowering year-round (or nearly).

Eupatorieae are distinguished by the combination of discoid heads, anther bases non-tailed (obtuse, rounded, or truncate), styles usually more or less filiform, style-branch appendages usually terete to clavate, and leaves usually opposite (FNAEC 2006a). *Praxelis* keys to either *Fleischmannia* Schultz-Bip. or *Chromolaena* DC. in FNAEC (2006b), matching key features for both—ca. 20 unequal phyllaries (the outer ones are generally smaller), 25–30 florets per head, a 3–4 ribbed achene, a pappus of ca. 40 capillary non-plumose bristles, and a glabrous style base. *Praxelis* has been reported as an annual and a perennial (U.S. Forest Service 2007; Waterhouse et al. 2003) and may behave as either, depending on local climate. A modified key is provided here, based on species in North America that look most similar to *Praxelis clematidea*, i.e., other herbaceous traditional *Eupatorium* L. s.l. with petiolate, opposite leaves trinerved from base and bluish purple corollas. For certainty of identification in a broader taxonomic context in the absence of comparative herbarium material or consultation with a specialist, the best references are the keys and descriptions in Cronquist (1980), King and Robinson (1987), FNAEC (2006a, 2006b), or, for Florida, Wunderlin and Hansen (2003).

FIG. 1. *Praxelis clematidea*. A. Inflorescence structure with inset of leaf. B. Close-up of flowers. C. Close-up of heads showing conical receptacle.

ARTIFICIAL KEY TO DISTINGUISH *PRAXELIS CLEMATIDEA* FROM SIMILAR GENERA IN NORTH AMERICA NORTH OF MEXICO

1. Receptacle conical (usually strongly so).
   2. Pappus lacking, coroniform (flat scales fused into a crown-like structure), or of 5–6 flattened scales (sometimes 5–6 tapering setae in *A. conyzoides*) **Ageratum**
      [20–125 florets; 30–40 phyllaries, (sub-)equal, persistent; *Ageratum* stems are sometimes decumbent; only 4 spp. in North America, 3 are discussed below, the fourth, *A. corymbosum* Zucc., occurs in AZ and NM].
   2. Pappus of capillary bristles; bristles more than 20.
      3. Bristles ca. 30; florets 35–70+; phyllaries ca. 25, subequal, persistent **Conoclinium**
         [3 spp.; 1 discussed below, the other 2 are *C. dissectum* A. Gray of TX, AZ, and NM and *C. betonicifolium* (Miller) R.M. King & H. Rob. of TX].
      3. Bristles ca. 40; florets 25–30; phyllaries 15–25, unequal, deciduous (absence apparent in fruit) **Praxelis**
         [13 spp. besides *P. clematidea*, all known only from South America].
1. Receptacle flat to slightly convex (rarely very shallowly conical in *Fleischmannia*).
   4. Phyllaries deciduous, 18–65, unequal; bristles ca. 40; florets 6–75 **Chromolaena**
      [only 4 spp. in North America, 3 discussed below, plus *C. bigelovii* (A. Gray) R.M. King & H. Rob., a shrub of TX]
   4. Phyllaries persistent, 20–30, unequal (to rarely subequal); bristles 20–40 (rarely 0 or 5), florets (10–)15–25(–50) **Fleischmannia**
      [only 2 spp. in North America, 1 discussed below, the other is *F. sonorae* (A. Gray) R.M. King & H. Rob. of AZ & NM]

Despite superficial macro-morphological similarity, the genera in the above key are from several different subtribes and do not form a clade (Schilling et al. 1999; Schmidt & Schilling 2000): Ageratinae (*Ageratum*), Fleischmanniinae (*Fleischmannia*), Gyptidinae (*Conoclinium*), Praxelinae (*Chromolaena* & *Praxelis*). Most North American regions don't have more than one or two of these *Praxelis* "look-alikes," but a total of eight species in all four genera is present in Florida: *Ageratum conyzoides* L. (native to tropical America; rare exotic in southern Florida), *A. houstonianum* Mill. (native to Mexico and northern Central America; occasional exotic in central and southern Florida), *A. littorale* A. Gray (rare in the keys; vegetatively glabrous, unlike most individuals of the other taxa here), *Chromolaena frustrata* (B.L. Rob.) R.M. King & H. Rob. (rare in southern Florida), *C. ivifolia* (L.) R.M. King & H. Rob. (native to tropical America; rare exotic in central Florida), *C. odorata* (L.) R.M. King & H. Rob. (occasional in southern Florida), *Conoclinium coelestinum* (L.) DC. (common throughout), and *Fleischmannia incarnata* (Walter) R.M. King & H. Rob. (occasional in northern and central Florida). In central Florida where *Praxelis* is now known, the most similar species to *Praxelis* that are most likely to be encountered are *Ageratum houstonianum*, *Conoclinium coelestinum*, and *Fleischmannia incarnata*, although *Chromolaena odorata* is also a possibility. See the following appendix for supplemental descriptions of taxa similar to *Praxelis*.

APPENDIX

SUPPLEMENTAL DESCRIPTIONS

The following descriptions are based on field and herbarium observations. This information supplements descriptions in Cronquist (1980) and FNAEC (2006b). All of these species are very different looking when placed side by side. These generalizations are designed to capture the important macroscopic differences and are offered here to facilitate preliminary field diagnoses. *Ageratum conyzoides, A. houstonianum, Praxelis clematidea,* and some individuals of *Chromolaena odorata* and *Conoclinium coelestinum* are conspicuously hairy to the naked eye (primarily just on the uppermost stem in the latter two). The hairs in *Fleischmannia incarnata* and many individuals of *Chromolaena odorata* and *Conoclinium coelestinum* are small enough and sparse enough to escape detection by the untrained naked eye. *Chromolaena* flowers are often a very pale bluish with the overall head having a whitish appearance due to the whitish phyllaries (except for the conspicuous green striations from the veins), *Fleischmannia* flowers are often whitish with only a pinkish or bluish tinge, and the others (*Ageratum, Conoclinium,* and *Praxelis*) are generally a stronger bluish purple, although all species can rarely be white flowered. All of these taxa have a resinous odor (probably largely due to secondary compounds in the glands, which are often visible with magnification, on the lower leaf surface and other structures), but apparently, *Praxelis* has a much harsher, cat-urine-like odor (Waterhouse et al. 2003).

Ageratum conyzoides and **A. houstonianum** (virtually identical in overall appearance, at least to the naked eye).—Petiole very short, less than 1/4 blade length, to nearly as long as the blade; blade mostly broadly ovate, rounded to truncate or cordate at the base (sometimes with a small cuneately narrowing wedge of tissue at the apex of the petiole, but the blade rarely with a cuneately based appearance, except when the blade is more narrowly ovate); blade often nearly as wide as long; margin mostly very regularly, evenly, and shallowly crenate-serrate; heads more or less subglobose, often wider than tall (ca. 8–9 mm wide, 6–7 mm tall), in dense clusters; phyllaries not quite 1 mm wide, more or less flat (apex very narrowed, somewhat involute), fairly imbricate (sometimes small gaps between them in fruit), not conspicuously striate (although the pale whitish veins do stand out against the green phyllaries on some specimens).

Chromolaena odorata.—Petiole relatively short, generally only 1/4–1/3 (sometimes to nearly 1/2) the blade length; blade broadly to narrowly ovate, sometimes lanceolate, mostly cuneately narrowed at base (sometimes this is present as a large triangular wedge below the rounded to truncate broader portion); blade highly variable, from ca. 1/3 to more than half as wide as long; margin often coarsely, irregularly toothed, but the teeth can be shallow and fairly regular, or the blade may be entire; heads strongly cylindrical, much longer than wide (ca. 3–5 mm wide, 8–12 mm long), not in dense clusters; phyllaries about 1 mm wide, flat, densely imbricate, with conspicuous green striations from the veins.

Conoclinium coelestinum.—Petiole generally 1/4–1/2 the blade length; blade ovate to bluntly triangular, cordate to truncate at the base (sometimes with a small cuneately narrowing wedge of tissue at the apex of the petiole, but the blade rarely with a cuneately based appearance); blade more than half as wide as long (smaller leaves are usually almost as wide as long); margin regularly serrate to nearly dentate (sometimes coarsely toothed, sometimes very shallow and nearly crenate); heads more or less subglobose (ca. 4–5 mm wide and 3–4 mm tall), mostly in dense clusters; phyllaries very narrow (much less than 1 mm wide), almost acicular in appearance, very loosely imbricate, with conspicuous gaps between them, even in flower, not striated.

Fleischmannia incarnata.—Petiole often as long as the blade or longer (sometimes only 1/2 or 1/3 as long); blade mostly sharply triangular, sometimes blunt or ovate, mostly truncate at the base (sometimes rounded or with small cuneately narrowed wedge of tissue at apex of petiole); blade mostly more than half as wide as long; margin regularly dentate (sometimes with larger irregular teeth near base, sometimes with shallower rounded serrations, sometimes subentire, especially on upper stem); heads more or less subglobose (to ca. 6–7 mm wide and tall), clusters mostly fairly lax (few heads, not densely packed); phyllaries ca. 0.8–0.9 mm wide, flat, loosely imbricate, with conspicuous gaps, at least in fruit, not conspicuously striated (although veins quite clear with 10× magnification).

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EXOTIC SPECIES OF *CELTIS* (CANNABACEAE) IN THE FLORA OF NORTH AMERICA

Alan T. Whittemore

US National Arboretum
3501 New York Ave NE
Washington, DC 20002-1958 U.S.A.

ABSTRACT

Two species of *Celtis* are naturalized in North America. *Celtis australis* escapes locally in riparian woodland in the Sacramento Valley of northern California, while *C. sinensis* (new to the adventive flora of North America) escapes in a variety of habitats from widely separated sites in California and in the District of Columbia, with seedlings found up to 300 m from adult plants. Descriptions and illustrations of both species are provided.

RESUMEN

Dos especies de *Celtis* están naturalizadas en Norte América. *Celtis australis* escapa localmente en bosque riparios en el Valle de Sacramento del norte de California, mientras que *C. sinensis* (nueva para la flora adventicia de Norte América) escapa en una variedad de hábitats en sitios ampliamente separados en California y en el Distrito de Columbia, con plantas que se encuentran hasta a 300 m de las plantas adultas. Se aportan descripciones e ilustraciones de ambas especies.

The genus *Celtis* L. (Cannabaceae, traditional Ulmaceae; Sytsma et al. 2002) is a widespread group of ca. 60 or 70 species of trees and shrubs, about half growing in the north temperate zone. Several *Celtis* species are cultivated in North America. Most commonly cultivated are two native species, *Celtis occidentalis* L. (hackberry) and *C. laevigata* Willd. (sugarberry). Two exotic species, *C. australis* L. (native to the Mediterranean basin and southwest Asia; Browicz and Zieliński 1982; Tutin 1991; Zieliński 1979) and *C. sinensis* Pers. (native to China and Japan; Fu et al. 2004), are available in the nursery trade. Both are planted, primarily as street trees, mainly in warm interior valleys of California (Brenzel 2001). *Celtis sinensis* is occasionally planted in the eastern United States (Meyer et al. 1994; Dirr 1998), and is sometimes considered a species with potential for more widespread use as a landscape tree (Dirr 1998).

Native *Celtis* species are well known to be weedy in gardens and disturbed urban areas. The single report of *C. australis* escaping in Butte Co., California by Oswald (1994) is the only report of a non-native *Celtis* sp. reproducing outside of cultivation in North America. No exotic species of *Celtis* is treated in any continental or regional flora for North America (Barker 1997; Wilken 1993). However, Batianoff and Butler (2002) considered *Celtis sinensis* one of the worst invasive plants in south-east Queensland, Australia, where they found it capable of crowding out native vegetation and forming monocultures, suggesting that the species has the potential to become invasive in suitable conditions.

Herbarium specimens and field sites for *Celtis* were examined. Several field sites in California were confirmed for *C. australis* and *C. sinensis*. The latter was also found to escape in a single location in the District of Columbia.

Nesom (2000) suggests a simple, uniform terminology for describing the "reproductive status and dispersive success" of non-native species. Uniform treatment of invasives is certainly necessary to allow meaningful comparisons between different works. However, the simple categories Nesom suggests are often difficult to apply to newly escaping woody plants or other perennials with long generation times. Distinguishing between Nesom's categories of "waif" and "naturalized" depends on the scientists' estimate of the long-term reproductive behavior of the species in the habitat. This is often suitable for annuals or perennials that are short-lived or reproduce when young, but not suitable for woody plants, where it may be many years before the long-term ability of a population to persist and reproduce in the habitat can be estimated accurately—thus, before it can be known whether the population is naturalized. Unfortunately, the early

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establishment phase is precisely the period when information about invasive tendencies of the species is most needed. It becomes important to document the habitats these species colonize and record their dispersal distances from seed sources. Invasive species have often gone unrecognized for long periods because they are not included in regional herbaria, floras, or other literature (Luken & Thieret 1995; Whittemore 2004). These two species are not described or illustrated in any North American flora (except McMinn & Maino 1947, who included *C. australis* as a cultivated species). A key, descriptions and illustrations are provided below to ensure that their populations can be recognized by local botanists.

TAXONOMIC TREATMENT

Identification of *Celtis* in North America is greatly complicated by unresolved taxonomic problems in a variable complex of shrubs and small trees, distributed over most of the United States, that are probably apomictic (Whittemore 2005a). These plants (referred to as the "small tree complex" below) are treated in different floras under a variety of names (the most commonly used, in the order they were first published, are *Celtis pumila* Pursh, *C. tenuifolia* Nutt., *C. reticulata* Torr., *C. lindheimeri* Engelm. ex K. Koch, and *C. georgiana* Small). None of the published treatments presents the variation in these plants adequately. Furthermore, of the five names listed above, only *C. pumila* and *C. reticulata* have been typified, and the correct application of the other names is in question. Until an adequate taxonomic treatment of this complex is available, it is not possible to write a full key to the North American species of *Celtis*. Furthermore, *Celtis* shows a very high level of within-plant leaf polymorphism, which greatly complicates identification. Leaves of juvenile or highly stressed plants are often very different from leaves of normal adults with the same genotype, and leaves of vigorous leaders may be much larger than leaves of fruiting laterals, and these two leaf types may differ very strongly in shape, especially in *C. occidentalis* and species of the small tree complex. Reliable identification of *Celtis* spp. may require studying fertile material, and comparing leaves that are subtending pedicels (Fernald 1950, Whittemore 2005b). The key below includes all *Celtis* species that grow outside of cultivation in the United States and Canada, but does not attempt to divide the small tree complex into natural taxa. For the taxonomy of *Celtis* subg. *Mertensia* (Kunth) Planch., see Berg and Dahlberg (2001).

1. Stems with prominent nodal spines. Flowers in dense cymes, hermaphroditic flowers with many male flowers lower on the same cyme (branch scars visible on pedicel). Styles bisbifid (i.e. each lobe is again deeply divided) ____ **Celtis** subg. **Mertensia**
  2. Nodal spines straight. Leaves 1–3(–5) × 0.4–2 cm. Axils of basal veins with deeply invaginated domatia. Shrubs 2–6 m tall. Florida, Texas, New Mexico, Arizona ____ **Celtis ehrenbergiana** (Klotzsch) Liebm. (=*Celtis pallida* Torr.)
  2. Nodal spines curved. Leaves 5.5–10 × 2.5–4 cm (to 13 × 6 cm in the tropics). Axils of basal veins without domatia. Shrubs (often scandent) 5–12 m tall. Florida ____ **Celtis iguanea** (Jacq.) Sarg.
1. Stems unarmed. Hermaphroditic flowers solitary on axillary pedicels (without branch scars on pedicel). Styles bifid (i.e. with two undivided lobes) ____ **Celtis** subg. **Celtis**
  3. Abaxial surface of leaf uniformly pubescent over its whole surface, felty to the touch; leaf abruptly contracted to a slender acumen, each margin with 20–32 teeth ____ **Celtis australis**
  3. Not as above: either abaxial surface of leaf with hairs confined to veins and vein axils, smooth to the touch, or the leaf blade evenly tapered or gradually narrowed to the slender acumen and entire or with no more than 16 teeth on each side.
    4. Large shrubs or small trees to 12 m tall, with leaning trunks and horizontal or arching leaders or (with age) multiple spreading trunks. Pollen largely or entirely aborted, seldom more than 10% of the grains stainable with acetocarmine, stainable grains (if present) very variable in size and number of pores, or else anthers remaining small and indehiscent. **"Small tree complex"**
    4. Excurrent trees to 30 m tall, typically with one strong vertical trunk (occasionally 2 or 3 parallel upright trunks), if small then with erect leaders. Anthers always dehiscent, pollen grains uniform in size, uniformly 3-porate, 95–100% stainable with acetocarmine.
      5. Leaves subtending pedicels ovate to ovate-elliptic, acute or short-acuminate, basal secondary veins extending (0.5–)0.6–0.75 length of blade; bark without corky outgrowths ____ **Celtis sinensis**
      5. Leaves subtending pedicels lanceolate, obliquely triangular or triangular-ovate, acuminate (usually slenderly so), basal secondary veins extending 0.3–0.55 length of blade; bark with prominent corky warts and ridges.

6. Leaves generally bright green on both surfaces; leaves subtending pedicels evenly tapering or gradually narrowed to the slender acumen; leaves of vigorous leaders larger but similar in shape; mature drupes 6–8 mm in diameter, brownish-orange or red __________ **Celtis laevigata** Willd.
6. Leaves generally paler abaxially; leaves subtending pedicels abruptly narrowed to the acumen; leaves of vigorous leaders larger and different in shape (often lanceolate or oblong, apex acute or short-acuminate, base often shallowly cordate); mature drupes 8–11 mm in diameter, dark brownish purple or purplish red (but immature drupes may be red or orange) ______ **Celtis occidentalis** L.

Celtis australis L., Sp. Pl. 1043. 1753. (**Fig. 1a**).
Deciduous trees to 20(–25) m tall. Bark gray, smooth or finely roughened. Branchlets brown or purplish, pubescent with spreading hairs to 0.5 mm long. Winter buds brown or purplish, 3–5 mm long, puberulent. Stipules linear or lanceolate, 3–6 mm, pubescent, fugacious. Leaves subtending pedicels with petiole 9–17 mm, tan, pubescent, dorsal sulcus usually a narrow sharp groove, seldom broad and shallow; leaf blade narrowly elliptical to lanceolate or lance-ovate, 8–11 × 3–5 cm, rather thick but flexible, adaxial surface dull dark green, abaxial surface light green or glaucous, pubescent with spreading hairs over veins and whole blade, felty to the touch; secondary veins 2–4 on each side, basal secondary veins extending (0.45–)0.5–0.7 length of blade; base cuneate to rounded, usually strongly asymmetrical, margin serrate from base to apex with sharp teeth 2–3 mm long, teeth 20–32 on each side; leaf apex abruptly contracted to a slender acumen; leaves of sterile leaders similar but often larger, to 16 cm long. Male flowers fascicled in axils of bud-scales and lower leaves, bisexual flowers solitary in lower leaf axils, reaching anthesis as leaves emerge in the spring. Pollen not seen. Drupes 1 per leaf axil, pedicel pubescent (at least proximally), 19–31 mm long, 1.6–2.7 times as long as subtending petiole. Drupe subglobose to pyriform, usually tapering to style-base, 10–12 mm in diameter, very dark brown (almost black) at maturity.

Distribution and Flowering.—Found in North America in riparian woodland, elev. 15–60 m. Flowering as leaves emerge in the spring; fruiting mid- to late fall.

Feral North American specimens examined. **U.S.A. California. Butte Co.:** spontaneous in riparian *Quercus lobata* - *Platanus* forest, Lower Bidwell Park between the nature center and Chico Creek, 39° 45' N, 121° 49' W, *A.T. Whittemore 06-004* (NA, UC). Tree ca. 8 m tall, edge of undeveloped woodland 10 m S of footbridge at W edge of golf course, Upper Bidwell Park, Chico, *V. Oswald 417* (CHSC). **Yolo Co.:** Spontaneous trees in dense secondary woods on banks of waterway (formerly a tributary of Willow Slough but now an artificial channel that drains north into the Willow Slough Bypass) just east of F street near jct. Faro Ave., 38° 34' N, 121° 44' W, *A.T. Whittemore 06-010* (NA, UC).

Celtis australis can be recognized by its smooth or finely roughened bark (not developing corky warts or ridges like the native North American species), its leaf blades that are sharply serrate and very slenderly long-acuminate from a narrowly elliptical to lanceolate or lance-ovate body and uniformly felty-pubescent beneath, and its large, dark brown or black drupes (the drupes ripen orange-brown, red or purplish in other American species).

Celtis australis was reported by Oswald (1994) as an escape in Bidwell Park, Chico, California. This site was visited in August 2006. The road between the site of the former Forestry Station and the current Nature Center is lined with large, well-established trees, evidently planted many years ago and now fruiting heavily. Seedlings and saplings are common in the vicinity of these trees. The majority are found in disturbed roadside habitats, but well-established small trees are also found in open *Quercus lobata* - *Platanus* woodland in the vicinity of the planted trees. Some of these trees are fruiting in this habitat, so *C. australis* is definitely established in native habitats and should be considered locally naturalized.

Feral plants of *Celtis australis* were also found along a waterway on the north side of Davis, in dense secondary forest that grew up on disturbed soil exposed when the waterway was channelized approximately thirty years ago. No cultivated trees were seen nearby, but the storm-drain system from much of Davis empties into this waterway, so seeds could easily have washed in from elsewhere in Davis (where *C. australis* is occasionally planted as a street tree). The land is not under cultivation, so under a strict application of the definitions of Nesom (2000) these trees are either waifs or naturalized (depending on their ultimate ability to reproduce themselves locally), but the site was heavily disturbed during the channelization, and it receives

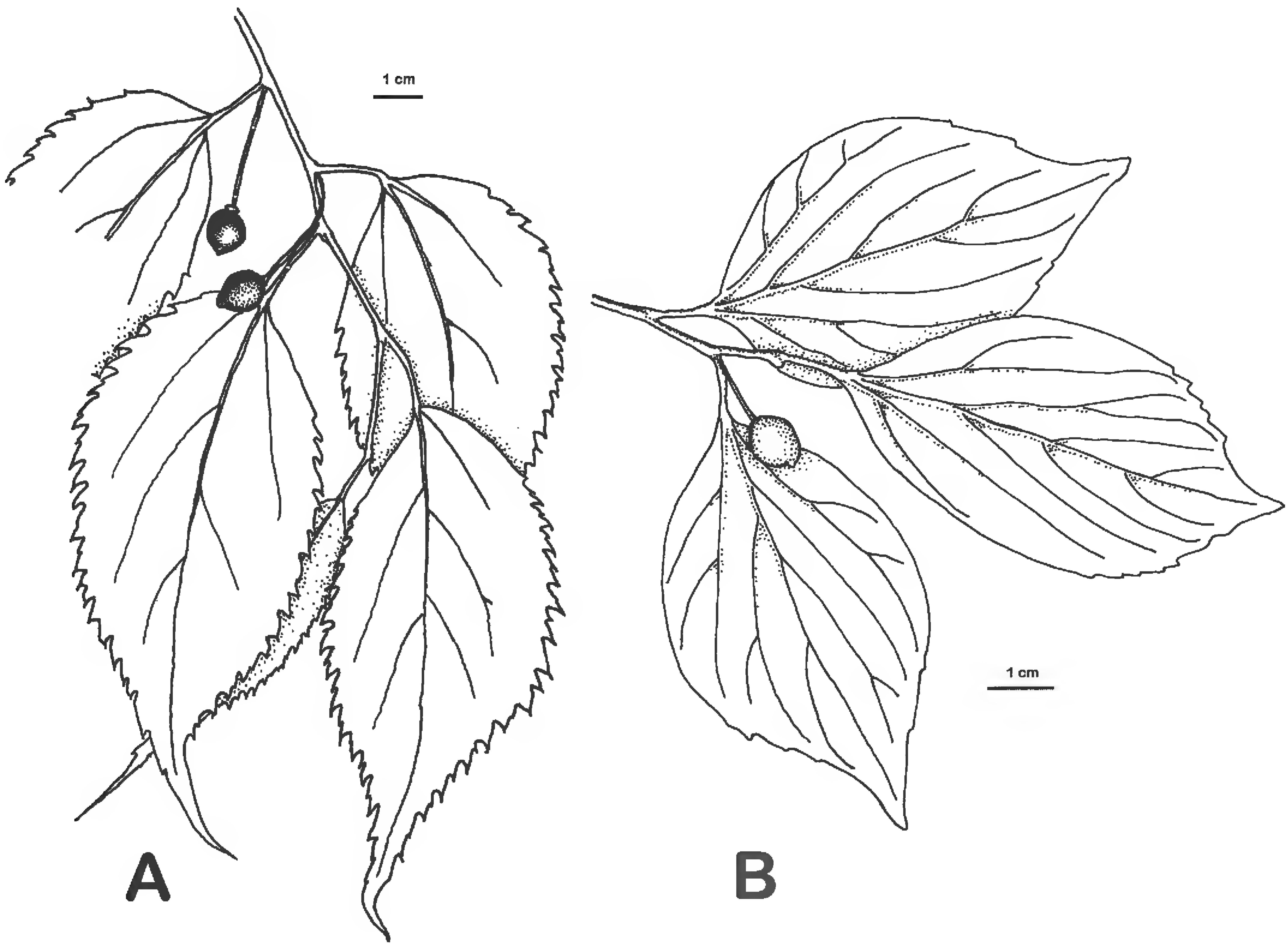

Fig. 1. Foliage and drupes of introduced *Celtis* species. A. *C. australis*. B. *C. sinensis*.

extra water from urban runoff, so it might be more realistic to regard them as weedy rather than invasive. The site is worth noting, however, as it does suggest that *C. australis* is capable of dispersing over significant distances.

Celtis sinensis Pers., Syn. Pl. 1:292. 1805. (**Fig. 1b**).
Deciduous trees to 20 m tall. Bark gray, smooth or finely roughened. Branchlets brown, brown-pubescent, sometimes becoming glabrescent late in season. Winter buds dark brown, 1–3 mm long, glabrous or puberulent. Stipules linear or lanceolate, 3–5 mm, pubescent, fugacious. Leaves subtending pedicels with petiole 3–10 mm, brown, pubescent, dorsal sulcus broad and shallow; leaf blade ovate to ovate-elliptic, 3–10 × 3.5–6 cm, rather thick but flexible, adaxial surface glossy dark green, abaxial surface light green, usually inconspicuously yellowish-brown puberulent when young, at maturity with hairs abaxially scattered on major veins and sometimes tufted in vein axils, smooth to touch, secondary veins 3–4 on each side, basal secondary veins extending (0.5–)0.6–0.75 length of blade; base rounded, obtuse, or obliquely truncate, subsymmetrical to moderately oblique, margin subentire to crenate on apical half, teeth 0–16 on each side, apex acute or short-acuminate; leaves of sterile leaders similar but often larger, to 9 cm long. Male flowers fascicled in axils of bud-scales and lower leaves, bisexual flowers solitary in lower leaf axils, reaching anthesis as leaves emerge in the spring. Anthers dehiscent, pollen grains uniform in size, uniformly 3-porate, 97–99% stainable with acetocarmine. Drupes 1(–3) per leaf axil, pedicel rather stout, pubescent (at least proximally), 4–10 mm long, 1–1.5 times as long as subtending petiole. Drupe subglobose, 5–7(–8) mm in diameter, brownish orange at maturity.

Distribution and Flowering.—Found in North America in riparian woodland, dry grassland, open woodland margins, elev. 15–580 m. Flowering as leaves emerge in the spring; fruits ripe mid- to late fall.

Feral North American specimens examined. **U.S.A. California. Butte Co.:** Occasional tree on E edge of Dry Creek in riparian woodland among sycamores, alders and willows, ca. 0.5 km N of jct. Pentz and Mesilla Valley Rds., elev. ca. 120 m, *B. Castro 436* (CHSC). **Orange Co.:** Weed tree invading UC Irvine Arboretum, UCI campus near intersection of Jamboree Blvd. and Campus Dr., elev. 15 m, *A.C. Sanders 27326* (UCR). **San Bernardino Co.:** Spontaneous in alder forest in canyon, Arrowhead Hot Springs and immediate vicinity; Coldwater Canyon and Strawberry Creek Canyon, ca. 0.5 mi E of the old Arrowhead Hot Springs Hotel, San Bernardino Mtns., elev. 580 m, *A.C. Sanders 13812* (UCR). **Yolo Co.:** Spontaneous trees to 5 m tall in dense secondary woods on banks of waterway (formerly a tributary of Willow Slough but now an artificial channel that drains north into the Willow Slough Bypass) just east of F street near jct. Faro Ave., 38° 34' N, 121° 45' W, *A.T. Whittemore 06-011* (NA, UC). Spontaneous tree 6 m tall in disturbed alkali grassland between road 101A and the railroad tracks, 0.6 km south of Road 29, north side of Davis, 38° 35' N, 121° 45' W, *A.T. Whittemore 06-012* (NA, UC). **District of Columbia:** Disturbed woodland margins, service road to Administration and Bonsai Pavilion loading docks, United States National Arboretum, 38° 55' N, 76° 58' N, *A.T. Whittemore 04- 012* (NA). Disturbed woodland margins near Administration Building parking lot, United States National Arboretum, 38° 55' N, 76° 58' N, *A.T. Whittemore 04- 016* (NA).

Celtis sinensis can be recognized by its smooth bark, its rather leathery, glossy leaves, with the margins usually crenate or bluntly serrate and the apex often rounded-acute.

Celtis sinensis has never been reported to escape in North America, but field sites and herbarium specimens were found documenting feral populations over a surprisingly wide geographic range and in a variety of habitats. It is not common at any of the sites and there is currently no evidence that it can be an aggressive competitor in our flora (as reported for Australia; Batianoff and Butler 2002), but saplings are often found several hundred meters from possible seed sources, suggesting that effective dispersal agents for this species exist in North America. On the grounds of the U. S. National Arboretum in Washington DC, young trees are occasionally found in open margins of native deciduous forest, often 100–300 m from the nearest possible seed source, but feral plants have not been observed in closed forest (except as a weed in cultivated beds). The Butte County site (*Castro 436*) is riparian woodland in dry, grassy low foothills of the northern Sierra Nevada, and according to the herbarium label, the feral plants are ca. 200 m from planted trees of *C. sinensis*. The tree near Road 101A in Yolo County (*Whittemore 06-012*) is in native alkali grassland that has never been cultivated but has probably been subject to some disturbance because of its proximity to the county road and railroad. This tree is at least 300 m from the nearest possible seed source. The long dispersal distances seen at most of the sites are not surprising, since the sweet, fleshy drupes are well suited to bird dispersal. Fleshy bird-dispersed fruit has been shown to be a significant predictor of invasive behavior in woody plants (Widrlechner et al. 2004), so further tracking of this species is desirable.

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LUZIOLA SUBINTEGRA (POACEAE: ORYZEAE), NEW TO FLORIDA AND THE UNITED STATES

John M. Kunzer

Department of Biology
University of South Florida
4202 E. Fowler Ave, SCA 110
Tampa, Florida 33620-5200, U.S.A.
kunzer@mail.usf.edu

Michael J. Bodle

South Florida Water Management District
3301 Gun Club Road
West Palm Beach, Florida 33406-3007, U.S.A.
mbodle@sfwmd.gov

ABSTRACT

The Neotropical graminoid taxon *Luziola subintegra* Swallen has been found in Fisheating Bay of Lake Okeechobee, Glades County, Florida, U.S.A. This represents the first known record of this taxon in both Florida and the United States. A description and modified key to the genus *Luziola* are given.

RESUMEN

El taxón neotropical graminoide *Luziola subintegra* Swallen se ha encontrado en la bahía Fisheating, del Lago Okeechobee, en el condado Glades, Florida, EE. UU. Esto representa el primer registro conocido de este taxón en la Florida y los Estados Unidos. Se presentan una descripción y clave modificada para el género *Luziola*.

In early December 2007, the USF herbarium received a specimen of an unknown aquatic grass collected along the northwestern shore of Lake Okeechobee, Glades County, Florida. The specimen was not satisfactorily identifiable as anything currently known in the state's flora (Wunderlin & Hansen 2003; Wunderlin & Hansen 2008) and its morphological characteristics led to investigation of the genus *Luziola*.

Examination of the revision of *Luziola* (Swallen 1965) revealed that there are two named species of very similar morphology, *L. spruceana* Benth. ex Döll and *L. subintegra* Swallen. The material in question was determined to be closer to *L. subintegra*, and this was confirmed by Gerrit Davidse (MO; determination in duplicate). Consultation of the Flora of North America treatment of *Luziola* (Terrell 2007) and the USDA PLANTS database (USDA, NRCS 2008) revealed that this taxon is also new to the United States flora.

Luziola subintegra has a known distribution from Mexico southward through Central America and South America southward to Argentina, and the Caribbean basin (Judziewicz et al. 2000). It is apparently rare in Central America, at least in Costa Rica and Nicaragua (Morales 2003; Pohl & Davidse 2001).

Description.—Stoloniferous perennial, emergent, floating, mat-forming aquatic or prostrate-creeping terrestrial. Culms prostrate, to ca. 1 m long or more, 3–10 mm diameter, rooting from the nodes. Leaf sheaths inflated, spongy; ligule an auriculate membrane, acuminate, 1–4 cm long; leaf blades 1–7.5 dm long, to 7–20 mm wide. Inflorescence monecious, staminate and pistillate portions in separate panicles or rarely with a few pistillate spikelets within the staminate panicle. Staminate panicle terminal, open; spikelets 5–7 mm long, with one fertile floret per spikelet; glumes absent or obsolete; palea 3-nerved; lemma 4 or 5-nerved, both palea and lemma hyaline, similar; anthers 6(5–7) per floret. Pistillate panicle axillary, congested, 1–several per culm, barely exserted from the sheath, the primary branches sharply recurved when mature, with evident pulvini, spikelets 3–5.5 mm long, with one fertile floret per spikelet; glumes absent or obsolete; palea 5-nerved; lemma 5–7-nerved, palea and lemma similar. Caryopses (achenes) with a hard, brittle pericarp, minutely longitudinally striate, asymmetrically ovoid, to 2 mm long, with a persistent style base.

Luziola subintegra is unlike any other *Luziola* currently known to the United States. It is robust, with large, thick culms, and has leaves with inflated, spongy sheaths and long, broad blades. All of our other *Luziola* taxa can be described as delicate, slender plants with narrow culms, and shorter, narrower leaves. *Luziola subintegra* gives the overall impression of being quite similar in habit to *Paspalum repens* P.J. Berguis or to a lesser degree *Hymenachne amplexicaulis* (Rudge) Nees (Figs. 1–3).

Fig. 1. ***Luziola subintegra*** **staminate panicle.**

Fig. 2. ***Luziola subintegra*** **pistillate panicles (upper–flowering, lower–mature).**

The following key modified from Wunderlin and Hansen (2003) serves to differentiate *L. subintegra* from the rest of the genus in Florida and the United States.

MODIFIED KEY TO *LUZIOLA*

1. Culms robust, 3 mm in diameter or larger; leaf blades 7 mm wide or wider; ligules 1–4 cm long ________ **L. subintegra**
1. Culms slender, 2 mm or less in diameter; leaf blades less than 6 mm wide; ligules less than 6 mm long.
    2. Inflorescence a raceme; pistillate spikelets mostly included in the subtending sheath ________ **L. fluitans**
    2. Inflorescence a panicle; pistillate spikelets all or mostly exserted from the subtending sheath.
        3. Pistillate spikelet 2–2.5 mm long; fruit smooth ________ **L. peruviana**
        3. Pistillate spikelet 3–5 mm long; fruit striate ________ **L. bahiensis**

In late December 2007, we investigated the extent of the population within Fisheating Bay, and found it to be nearly ubiquitous there. The population consisted of two large, near-monoculture mats, one mat of ca. 2 ha, to the east of Harney Pond Canal, and the other of ca. 80 ha, to the west of the canal (Fig. 3). The locality of these two mats was within a portion of the lake bed that during the record low-water level of early June 2007 was completely exposed and bare of all vegetation. Surrounding each of the large mats and scattered throughout the open bay were sporadic, small clumps of one to several mature individuals. It was also found as both an emergent aquatic and a terrestrial inside the mouth of Fisheating Creek. At this location, the terrestrial individuals of a mature state were evident only in small, isolated clumps, and they appeared to be less competitive against the other terrestrial flora.

Fisheating Creek is the only remaining unregulated inflow to Lake Okeechobee. Based upon this information and the fact that *L. subintegra* is present in the creek, we speculate that Fisheating Creek is its point of introduction into Fisheating Bay and Lake Okeechobee. Given the extent of the current population and

FIG. 3. ***Luziola subintegra*** **population W of Harney Pond Canal, from center of population, facing SW.**

the plant's apparent fecundity, we suggest that this taxon be considered for listing by the Florida Exotic Pest Plant Council (FLEPPC). We also suggest that ecological research be immediately undertaken to determine its potential impact on Florida's natural systems.

Voucher specimens: **U.S.A. FLORIDA. Glades Co.:** Lake Okeechobee, Fisheating Bay, ca. 3.75 km S of the junction of C-721 and FL 78. 26° 58' 0.3" N, 81° 04' 9.5" W, 6 Dec 2007, *Mike J. Bodle s.n.* (MO, USF 244612, others to be distributed); Lake Okeechobee, Fisheating Bay, ca. 3.25 km SE of the junction of C-721 and FL 78. 26° 58' 13.8" N, 81° 03' 37.4" W, 20 Dec 2007, *John M. Kunzer, Mike J. Bodle, Kurt Ramsey 2253* (USF 244608, others to be distributed).

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NEW AND NOTEWORTHY RECORDS OF SEVERAL NON-NATIVE VASCULAR PLANT SPECIES IN ARKANSAS

Brett E. Serviss
Department of Biology
Henderson State University
Arkadelphia, Arkansas 71999-0001, U.S.A.
servisb@hsu.edu

James H. Peck
Department of Biology
University of Arkansas at Little Rock
Little Rock, Arkansas 72204, U.S.A.
jhpeck@ualr.edu

ABSTRACT

Collections of nine species of vascular plants, all non-native to the United States, are reported as new or noteworthy for Arkansas. Three species, *Marsilea quadrifolia*, *Pennisetum setaceum*, and *Thunbergia alata*, are reported as new to Arkansas. *Amaranthus blitum* and *Chamaesyce ophthalmica* are reported for their second occurrence in Arkansas. An additional county record for each of three federally listed invasive species is reported: *Eichhornia crassipes*, *Hydrilla verticillata*, and *Myriophyllum spicatum*. The current known distribution of *Quercus acutissima* in Arkansas is provided. Finally, some instances of localized reproductive spontaneity originating from cultivated plants are reported. These include: *Acer palmatum* (Japanese maple), *Camellia japonica*, (common camellia), *Camellia sasanqua* (fall-flowering camellia, *Loropetalum chinense* (fringe flower), *Raphiolepis indica* (Indian hawthorn), and *Ternstroemia gymnanthera* (cleyera); all of which were previously undocumented in Arkansas in this condition.

RESUMEN

Se citan como nuevas o reseñables las colecciones de nueve especies de plantas vasculares, todas ellas no-nativas de los Estados Unidos, para Arkansas. Tres especies, *Marsilea quadrifolia*, *Pennisetum setaceum*, y *Thunbergia alata*, se citan como nuevas para Arkansas. *Amaranthus blitum* y *Chamaesyce ophthalmica* se citan por segunda vez en Arkansas. Se da una cita adicional para un condado de tres especies de la lista federal de especies invasoras: *Eichhornia crassipes*, *Hydrilla verticillata*, y *Myriophyllum spicatum*. Se aporta la distribución actual de *Quercus acutissima* en Arkansas. Finalmente, se citan algunos ejemplos de reproducción espontánea de plantas cultivadas. Estas incluyen: *Acer palmatum* (arce japonés), *Camellia japonica*, (camelia común), *Camellia sasanqua* (camelia de otoño), *Loropetalum chinense* (flor de flecos), *Raphiolepis indica* (espino indio), y *Ternstroemia gymnanthera* (cleyera); que no estaban documentados en Arkansas en esta condición.

INTRODUCTION

Non-native species are continually introduced into the United States through both accidental and intentional human activities. These introductions sometimes lead to the formation of spontaneous populations of these plants. Spontaneous is here defined as the autonomous occurrence through sexual or asexual reproduction of a non-native plant species in a region or flora to which it is not native. It is equivalent to the term "escaped" as defined by Nesom (2000). Most non-native species subsequent to introduction do not successfully establish, or if establishment occurs, do not pose a serious threat to native plant species or ecosystems (Williamson 1996). However, some of these introduced species become invasive, and sometimes sufficiently so to reduce native biodiversity. It is therefore important to record first encounters with escaped populations and monitor these new spontaneous occurrences of non-native species to evaluate their potential for becoming the next wave of invasive species (Yatskievych & Raveill 2001). At present, non-native species comprise approximately 21% of the Arkansas flora (Arkansas Vascular Flora Committee 2006), with 3% annotated as invasive in Arkansas.

Our field work focusing on ruderals and recent escapes in urban environments has led to the recognition of many non-native plant species being documented as new to Arkansas (Peck 2003; Peck & Serviss 2006; Serviss et al. 2006, 2007a, 2007b), with many of the species locally well established when discovered. At present, more species are being documented as entering the Arkansas flora than are being lost from habitat loss, fragmentation, or human disturbance. Additionally, we have observed numerous instances of localized reproductive spontaneity in several species of non-native ornamental shrubs, and while the parent plants were cultivated, substantial reproduction of offspring was documented in the local vicinity of these plants (see end of paper for specimen data).

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The national occurrence and distribution of the below listed taxa was determined from the national flora database kept by NRCS (1999).

SPECIES NEW OR NOTEWORTHY FOR ARKANSAS

Amaranthus blitum L. (Amaranthaceae). Purple amaranth is a ruderal species that is native to the Mediterranean region. It occurs across the coastal states from Massachusetts south to Florida, and west to Louisiana and Texas. This is only the second record for *A. blitum* in Arkansas; it was previously documented in Pulaski County (Peck & Serviss 2006).

Voucher specimens: **Clark Co.:** several reproductively mature plants as weeds in flower bed, Lake DeGray Visitor Center, Lake DeGray State Park, 28 Oct 2007, *Serviss 7344* (HEND); urban ruderal habitat, Arkadelphia, Henderson State University campus, 25 Aug 2004, *Serviss 6124* (HEND).

Chamaesyce ophthalmica (Pers.) D.G. Burch (Euphorbiaceae). Florida hammock sandmat is an annual ruderal species that is native to the Gulf coast from Florida and Georgia west to Louisiana. This is only the second record for *C. ophthalmica* in Arkansas; it was previously documented in Pulaski County (Peck & Serviss 2006).

Voucher specimen: **Clark Co.:** several reproductively mature plants as weeds in flower bed, Lake DeGray Visitor Center, Lake DeGray State Park, 28 Oct 2007, *Serviss 7345* (HEND).

Eichhornia crassipes (Mart.) Solms (Pontederiaceae). Water hyacinth, which is native to Brazil, is an aggressive and invasive non-indigenous aquatic species in North America. It was reported as present and then eradicated twice in Arkansas, once as an escape in southeastern Arkansas and once in southwestern Arkansas (Tumlison & Serviss 2006). It is here reported as a persisting and spreading population at its most northerly location yet in Arkansas, at the junction of the Little Maumelle River and the Arkansas River in Pulaski County, Arkansas. Here it co-occurred with *Egeria densa*, *Hydrilla verticillata*, *Marsilea quadrifolia*, and *Myriophyllum spicatum*. It was first discovered at this location in 2006 by Bob Spraggins, an accountant for the Arkansas Natural Heritage Commission, who brought it to the attention of Theo Witsell, staff botanist of the same agency. In 2007 the locality was searched, and all five invasive species were noted as unchecked and spreading.

Voucher specimen: **Pulaski Co.:** a floating-plant emergent spreading along 4 km of swamp, slough, and shore habitats of the lower Little Maumelle River, 16 Jul 2007, Peck *07-1352* (LRU).

Hydrilla verticillata (L.f.) Royle (Hydrocharitaceae). Water-thyme is an aggressive and invasive non-indigenous aquatic species that is native to Asia. It was reported as present in several impoundments of tributary rivers to the Arkansas River (Peck 2003; Peck & Serviss 2006), and here for the first time in Pulaski County, at its most northerly location yet in Arkansas, at the junction of the Little Maumelle River and the Arkansas River. Here it co-occurred with *Egeria densa*, *Eichhornia crassipes*, *Marsilea quadrifolia*, and *Myriophyllum spicatum*. It was discovered at this location in 2007 with four other invasive species and was noted as unchecked and spreading. As it is known to survive multiple winters as far north as Iowa (Peck & Smart 1986), it might also be found in northern Arkansas impoundments.

Voucher specimen: **Pulaski Co.:** a submerged aquatic plant spreading along four km of swamp, slough, and shore habitats of the lower Little Maumelle River, 16 Jul 2007, *Peck 07-1358* (LRU).

Marsilea quadrifolia L. (Marsileaceae). European Waterclover is native to Europe and Asia, and is an aggressive and invasive non-indigenous aquatic species. It was introduced into eastern North America as an aquarium plant, and has since escaped and spread westward as far as southwestern Iowa. It is reported for the first time from Arkansas, where it was found along a muddy shore of the Little Maumelle River, Pulaski County, Arkansas. The patch was relatively small, suggestive of a recent introduction, most likely by transient waterfowl. It was associated with extensive growths of other non-native and invasive species: *Eichhornia crassipes*, *Egeria densa*, *Hydrilla verticillata*, and *Myriophyllum spicatum*.

Voucher specimen: **Pulaski Co.:** a single patch of floating-leaf shoreline plant spreading along muddy, disturbed shore habitat of the Little Maumelle River near Pinnacle Valley Bridge two km upstream of the mouth of the Little Maumelle River at the Arkansas River, 16 Jul 2007, *Peck 07-1514* (LRU).

Myriophyllum spicatum L. (Haloragaceae). Eurasian water milfoil is an aggressive and invasive non-indigenous aquatic species that is native to Europe and Asia. It is reported for the first time in Pulaski County, at the junction of the Little Maumelle River and the Arkansas River. Here it co-occurred with *Eichhornia crassipes*, *Egeria densa*, *Hydrilla verticillata*, and *Marsilea quadrifolia*.

Voucher specimen: **Pulaski Co.:** a submerged plant spreading along shore habitats along four km of the Little Maumelle River down to Twin Rivers County Park at the mouth of the Little Maumelle River at the Arkansas River, 9 Jul 2007, *Peck 07-1635* (LRU).

Pennisetum setaceum (Forsk.) Chiov. (Poaceae). Fountain grass is a caespitose, perennial grass that is native to Africa. This is the first documentation of this species in Arkansas outside of cultivation. It has been previously documented outside of cultivation in Arizona, California, Colorado, Florida, Hawaii, Louisiana, New Mexico, Oregon, and Tennessee.

Voucher specimen: **Clark Co.:** a few spontaneous plants growing as weeds in a shrub planting on the Henderson State University campus; the origin of the population is not known, and it did not persist for more than a couple of years, Arkadelphia, 24 Sep 2004, *Serviss 6636A* (HEND).

Quercus acutissima Carruthers (Fagaceae). Sawtooth oak is native to Korea, China, Japan, and Vietnam. It has been documented outside of cultivation in several states, including Alabama, Georgia, Louisiana, Maryland, North Carolina, Mississippi, Pennsylvania, and Virginia. Though previously documented as present in the Arkansas flora (Arkansas Vascular Flora Committee 2006); specifically, it has been documented outside of cultivation in 10 Arkansas counties (Cross, Drew, Hempstead, Jackson, Jefferson, Lincoln, Nevada, Pike, Union, and most recently, Clark). Sawtooth oak has demonstrated the ability to escape cultivation and subsequently naturalize in many areas of the eastern U.S., especially when cultivated plants are in the vicinity of open areas, such as grasslands and disturbed woods (Whittemore 2004). Hence, it appears to have the potential to become invasive in Arkansas, and its current known distribution in the state seems worthy of note.

Voucher specimen: **Clark Co.:** seven, spontaneous, juvenile plants growing around and under cultivated shrubs; a cultivated *Q. acutissima* tree was present some distance from the vicinity of the spontaneous juveniles, and it is possibly the parent, Arkadelphia, Ouachita Baptist University campus, 31 Oct 2007, *Serviss 7342* (HEND).

Thunbergia alata Bojer ex Sims (Acanthaceae). Blackeyed susan vine is native to Tropical Africa, but has become a pantropical weed. *Thunbergia alata* is currently only known outside of cultivation in the U.S. from Florida, Hawaii, and Texas. One spontaneous plant has been documented in Arkansas. This is the first documentation of this species in Arkansas outside of cultivation.

Voucher specimen: **Clark Co.:** a single, reproductive plant located in a somewhat unkempt lawn area of a home site, Arkadelphia, 420 Cedar Grove Road, 5 Sep 2004, *Serviss 6628* (HEND); one of the authors (BES) has known the homeowner at this location for several years, and during that time no material of *T. alata* has been present, cultivated or otherwise, on the homeowner's property.

ADDITIONAL NOTEWORTHY SPECIES

The following six non-native, woody, angiosperms were documented as spontaneous offspring in the immediate vicinity, or within a short (several meters) distance from the vicinity of cultivated and reproductive individuals of these species. Documentation of these initial reproductive successes by cultivated non-native plants is essential for dating their initial entrance into the flora by other than the direct assistance of human activities. Additionally, the ability of these species to successfully reproduce offspring is significant in that probably with regard to most of the non-native and invasive ornamentals in the U.S., their initial "entrance" into the flora was accomplished in similar fashion to the following examples. It is therefore crucial to recognize and subsequently document these initial occurrences of spontaneity in non-native plant species. All six of the following species have displayed successful reproduction in Arkansas, evidenced by the presence

of few to many spontaneous juveniles being present within a short distance of cultivated reproductive age plants of their respective species.

Specimen data: **Acer palmatum** Thunb. (Sapindaceae). Japanese maple is native to Japan, and has been previously recorded outside of cultivation in Ohio, Pennsylvania, and New York. Voucher specimen: Clark Co.: dozens of seedlings scattered across a few disturbed flower beds in proximity to cultivated plants of *A. palmatum*, Arkadelphia, Ouachita Baptist University campus, 27 Nov 2007, *Serviss 7352* (HEND). **Camellia japonica** L. (Theaceae). Japanese camellia is native to Japan, but has been documented outside of cultivation in Florida, Georgia, and the Carolinas. Voucher specimen: Clark Co.: a few spontaneous plants present beneath a large, cultivated shrub of *C. japonica*, Arkadelphia, Henderson State University campus, 1 Nov 2007, *Serviss 7344* (HEND). **Camellia sasanqua** Thunb. (Theaceae). Fall-flowering camellia is native to Japan. It has been documented outside of cultivation in Florida, Georgia, and the Carolinas. It has been documented in several locations of Clark County by the presence of numerous (more than 100) spontaneous seedlings and juveniles in the vicinity of cultivated *C. sasanqua* plants. Voucher specimens: Clark Co.: several small seedlings and juvenile plants in the vicinity of two reproductive age plants of the species, Arkadelphia, edge of disturbed wooded area off of 12th Street, one block west of the Henderson State University campus, 18 Mar 2005, *Serviss 6861* (HEND); Arkadelphia, Henderson State University campus, 29 May 2005, *Serviss 6985* (HEND). **Loropetalum chinense** (R. Br.) Oliv. (Hamamelidaceae). Fringe flower is native to China. Voucher specimen (two locations located for Clark Co.; one cited below): Clark Co.: several spontaneous seedling and juvenile plants growing in a disturbed area in the vicinity of several cultivated, reproductively mature plants of *L. chinense*, Arkadelphia, Henderson State University campus, Oct 2006, *Serviss 7094* (HEND). **Raphiolepis indica** (L.) Lindl. (Rosaceae). Indian hawthorn is native to China. Arkansas material of this species is represented by numerous spontaneous seedlings in the vicinity of reproductive age plants of the species (present at a couple of locations in Clark County). Voucher specimen: Clark Co.: numerous spontaneous seedlings and slightly larger juveniles in the vicinity of several cultivated, reproductively mature plants of *R. indica*, Arkadelphia, Henderson State University campus, 28 Feb 2007, *Serviss 7115* (HEND). **Ternstroemia gymnanthera** (Wight & Arn.) Sprague (Theaceae). Cleyera is native to India, the Malaysian Peninsula, and Japan. This species is known from Arkansas by only a few spontaneous juvenile plants (one specimen cited below). Spontaneous juvenile plants were found several meters from the vicinity of cultivated reproductive age plants of *T. gymnanthera*. Voucher specimen: Clark Co.: one juvenile plant growing with a variety of other weeds under cultivated shrubbery; cultivated, reproductive age plants of *T. gymnanthera* were present a short distance from the location of the spontaneous juvenile, Arkadelphia, residence adjacent to Henderson Street and 13th Street, 28 Feb 2007, *Serviss 7113* (HEND); circumstantial evidence indicates dispersal by birds (the seeds of *T. gymnanthera* are bird-dispersed).

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BOOK NOTICE

Douglas J. Futuyma, H. Bradley Shaffer, and Daniel Simberloff (eds). 2005. **Annual Review of Ecology, Evolution, and Systematics: Volume 36, 2005.** (ISBN 978-0-8243-1436-0, hbk; ISSN 1543-592X). Annual Reviews Inc., 4139 El Camino Way, P.O. Box 10139, Palo Alto, California 94303-0139, U.S.A. (**Orders:** www.annualreviews.org, science@annualreviews.org, 1-800-523-8635, 1-650-493-4400, 1-650-424-0910 fax). $79.00 indiv., 689 pp., indexes, 7 5/8" × 9 3/8".

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NOTEWORTHY VASCULAR PLANT COLLECTIONS FROM NORTHWEST LOUISIANA

Christopher S. Reid and Patricia L. Faulkner

Louisiana Natural Heritage Program
Louisiana Department of Wildlife and Fisheries
Baton Rouge, Louisiana 70898, U.S.A.

Barbara R. MacRoberts and Michael H. MacRoberts

Bog Research, 740 Columbia
Shreveport, Louisiana 71104, U.S.A.
and Herbarium, Museum of Life Sciences
Louisiana State University in Shreveport
Shreveport, Louisiana 71115, U.S.A.

ABSTRACT

The following four species are documented as new to Louisiana: *Sagittaria subulata*, *Senecio ampullaceus*, *Lechea san-sabeana*, and *Panicum diffusum*. Significant new records are provided for four species: *Grindelia lanceolata*, *Arabis canadensis*, *Geocarpon minimum*, and *Carex arkansana*. Species are listed alphabetically by family with comments and citation of voucher specimens.

RESUMEN

Las siguientes cuatro especies se documentan como nuevas para Louisiana: *Sagittaria subulata*, *Senecio ampullaceus*, *Lechea san-sabeana*, y *Panicum diffusum*. Se aportan nuevas citas significativas de cuatro especies: *Grindelia lanceolata*, *Arabis canadensis*, *Geocarpon minimum*, y *Carex arkansana*. Las especies se listan alfabéticamente por familia con comentarios y citación de especimenes testigos.

INTRODUCTION

Recent floristic work in northwestern Louisiana has resulted in the discovery of plants new to Louisiana and other significant records (Reid & Faulkner 2006; MacRoberts et al. 2007; Reid et al. 2007). In this paper we report four species new to Louisiana and four additional significant collections.

ALISMATACEAE

Sagittaria subulata (L.) Buchenau—*Sagittaria subulata* is not reported for Louisiana by USDA, NRCS (2007), Haynes and Hellquist (2000), Kartesz and Meacham (2005), MacRoberts (1984), or Thomas and Allen (1993). On 27 June 2006, we discovered hundreds of plants on a stretch of shoreline on Caddo Lake at Oil City, northern Caddo Parish. According to Haynes and Hellquist (2000), *S. subulata* ranges from Massachusetts south to Florida and west to Mississippi. Our record extends the range of *S. subulata* over 500 km to the northwest of its previously known western range limit in Mississippi.

Voucher specimens: **Caddo Parish:** along shore of Caddo Lake in Oil City, E1/2 SE1/4 S13 T20N R16W. lat/long 324319N, 935814W, open sunny lakeshore in saturated mucky sand, with *Eleocharis* (*microcarpa*?), *Nelumbo lutea*, *Panicum hemitomon*, *Hydrocotyle verticillata*, *Luziola fluitans*, *Potamogeton nodosus*, flowering plants on hammocks, 100s of submerged plants, 27 Jun 2006, *Reid 5809* (FSU, LSU); along shore of Caddo Lake immediately S of boat ramp in Earl G. Williamson Park, Oil City, flowers white, 11 Jul 2006, *L.R. Raymond 2166* (LSUS).

ASTERACEAE

Grindelia lanceolata Nutt.—*Grindelia lanceolata* is reported for Louisiana by Riddell (1852) and Steyermark (1934). Steyermark (1934) cites Leavenworth specimens at G (= GH) and NY as his authority. MacRoberts (1984) and Thomas and Allen (1996) include *G. lanceolata* in the Louisiana flora on the basis of these older literature reports. We discovered *G. lanceolata* on 20 June 2007 in two small saline prairie remnants in Sabine Parish. The plants occurred on open slicks with overall light vegetative cover. During a return visit on 7 August 2007, we observed an estimated 500 plants, many of which were beginning to flower. Our record of *G. lanceolata* is apparently the first in Louisiana since Leavenworth's time, ca. 150 years ago (Ewan 1968).

Voucher specimens: **Sabine Parish:** Oakley's Pasture (a.k.a. Mary Lee's Pasture), N of LA 174 ca. 5 mi W of Converse, along E side of McDonald Bayou, NW1/4 NW1/4 S12 & SW1/4 SW1/4 S1, T9N R14W. lat/long: 314711N, 934544W, common in small area of remnant

saline prairie on the more extreme end within a large area of former saline prairie that was converted to Bahia grass long ago, *Talinum parviflorum*, *Cynodon dactylon*, *Sporobolus pyramidatus*, *Evolvulus sericeus* etc., remnant ca. 0.25 acres, 20 Jun 2007, *Reid 6164*, *Faulkner et al.* (LSU); N edge of pine plantation adjacent to Oakley's Pasture (a.k.a. Mary Lee's Pasture), N of LA 174 ca. 5 air mi W of Converse, E side of McDonald Bayou, SE1/4 NE1/4 S11 T9N R14W. lat/long: 314658N, 934554W, several hundred plants in small saline prairie remnant with abundant *Croton willdenowii*, also w/ *C. capitatus*, *Neptunia lutea*, *Talinum parviflorum*, *Hypericum drummondii*, & *Helenium amarum*, 7 Aug 2007, *Reid 6211*, *Faulkner & Gregory* (LSU, LSUS, NO).

Senecio ampullaceus Hook.—*Senecio ampullaceus* is not reported for Louisiana by MacRoberts (1984), Thomas and Allen (1996), Kartesz and Meacham (2005), USDA, NRCS (2007), or Barkley (2006). On 28 March 2007, we discovered a population of *S. ampullaceus* in the xeric sandhills (M.H. MacRoberts & B.R. MacRoberts 2006) of northern Caddo Parish. It was recently reported new to Arkansas (Singhurst & Holmes 1998) and Oklahoma (Holmes et al. 2006). Our record is apparently the first for *S. ampullaceus* from Louisiana.

Voucher specimen: **Caddo Parish:** S side of Kendrick Road near its W terminus at Vivian-Atlanta Rd., near NE corner of S15 & NW corner of S14, T22N R16W. lat/long: 325420N, 935957W, sandy field with conspicuous *Opuntia humifusa*, 28 Mar 2007, *Reid 6020 & Faulkner* (LSU).

BRASSICACEAE

Arabis canadensis L.—On 13 April 2006, we discovered a small population of *Arabis canadensis* in De Soto Parish growing on a low ridge embedded in a matrix of poorly drained *Quercus similis* – *Crataegus* spp. flatwoods. MacRoberts (1989) and Thomas and Allen (1996) include *A. canadensis* in the Louisiana flora on the basis of a specimen collected by Leggett (*1578* – NLU) from Bossier Parish. Leggett (1976) reported it from one station in Bossier Parish where it was "localized and uncommon on sandy soil in mixed woods." During recent visits to NLU, we have failed to locate this specimen. It is apparently not on loan and may have been misfiled or annotated to another taxon. Providing that the identification and locality data are correct, our record is the second from Louisiana. If the Leggett specimen was misidentified, then our record is the first for the state. In either case, our record represents the only confirmed extant *A. canadensis* population in Louisiana.

Voucher specimen: **De Soto Parish:** Dickson Prairie, S side of Cypress Bayou, 2 air mi NE of Stonewall, NW1/4 S9 T15N R14W, mixed hardwood-loblolly forest on low ridge, associated with *Geum canadense*, *Pinus taeda*, *Aesculus pavia*, *Senecio obovatus*, *Celtis laevigata*, *Dioscorea villosa*, and *Sabal minor*, 13 Apr 2006, *Reid 5713 and Faulkner* (LSU); same locality, 2 May 2006, *Reid 5751*, *Faulkner et al.* (FSU, LSU).

CARYOPHYLLACEAE

Geocarpon minimum Mackenzie—*Geocarpon minimum* is federally listed as threatened and is known from Arkansas, Louisiana, Missouri, and Texas (Nienaber 2005). This species was initially discovered in Louisiana in Winn Parish in 1989 with an additional population discovered nearby in 1992 (McInnis et al. 1993). These were the only two Louisiana populations known until 2006 when a third occurrence was discovered in a saline prairie in Caddo Parish (B.R. MacRoberts & M.H. MacRoberts 2006). A survey for *G. minimum* in saline prairies in Caddo, De Soto, Red River, and Winn parishes was conducted in March 2007 (MacRoberts & MacRoberts 2007) that yielded three new sites representing two new populations, all in De Soto Parish. Because two of the collection sites, Dickson Prairie and Dalton Prairie, are separated by a narrow drainage, we regard *G. minimum* from these two sites as constituting a single population. The third collection was from another saline prairie, Rambin Bayou Prairie, which is well-removed from the other sites.

Voucher specimens: **De Soto Parish:** Dickson Prairie, ca. 2 air mi NE of Stonewall, NW1/4 S9 T15N R14W. lat/long: 321827N, 934824W, saline prairie in and around slicks and in sparsely vegetated areas. associated with *Opuntia humifusa*, *Talinum parviflorum*, *Plantago pusilla*, *Houstonia rosea*, *H. micrantha*, *Crassula aquatica* and *Anagallis minima*, 7 Mar 2007, *Reid 5995*, *Faulkner*, *MacRoberts & MacRoberts* (LSU); Dalton Prairie, ca. 2.5 air mi SE of Keithville, SE1/4 S4 T15N R14W, lat/long: 321841N, 934807W, saline prairie, in and around slicks and sparsely vegetated areas associated with *Opuntia humifusa*, *Plantago pusilla*, *Talinum parviflorum*, *Houstonia rosea* and *H. micrantha*, etc., 7 Mar 2007, *Reid 6003*, *Faulkner*, *MacRoberts & McRoberts* (LSU); Rambin Bayou Prairie, N side of Rambin Bayou, W of I-49 via gas field roads, NE1/4 S7 T14N R13W. lat/long: 321303N, 934351W, ca. 250 plants counted, in and around slicks with *Anagallis minima*, *Crassula aquatica*, *Nothoscordum bivalve*, *Krigia occidentalis*, *Plantago pusilla*, *Houstonia* spp., and *Talinum parviflorum*, 19 Mar 2007, *Reid 6010*, *Faulkner*, *& Smith* (LSU).

CISTACEAE

Lechea san-sabeana (Buckley) Hodgdon—*Lechea san-sabeana* was reported for Louisiana by Riddell (1852) as *Lechea drummondii* Torr. & A. Gray and was excluded from the flora by Thomas and Allen (1996). MacRoberts (1984) lists *L. san-sabeana* as questionable in Louisiana and cites the Riddell report. Correll and Johnston (1970), Carr (2002), Kartesz and Meacham (2005), and Diggs et al. (2006) regard *L. san-sabeana* as a Texas endemic. In May and June 2007, we collected *L. san-sabeana* at three saline prairies in De Soto and Caddo parishes. It was common at these sites and was associated with pimple (mima) mounds.

Voucher specimens: **Caddo Parish:** Barron Road Saline Prairie, T16NR14WS27, N of Barron Road, S of Boggy Bayou. Mima mounds, 13 Jun 2007, *B.R. & M.H. MacRoberts 7830* (LSU). **De Soto Parish:** Dickson Prairie, ca. 2 air mi NE of Stonewall, NW1/4 S9 T15N R14W. lat/long: 321827N, 934824W, abundant in and on edges of pimple mounds in high quality saline prairie, 4 May 2007, *Reid 6064, Faulkner & Smith* (TEX-LL); same locality, common on lower edges of pimple mounds, associated w/ *Iva angustifolia, Chamaecrista fasciculata, Rhynchospora harveyi, Helianthemum rosmarinifolium, Fimbristylis puberula, & Dichanthelium aciculare*, 21 Jun 2007, *Reid 6179, Faulkner, & Jones* (LSU, NO); Dalton Saline Prairie/Barren, T15NR14WS4, mima mounds, 12 Jun 2007, *B.R. & M.H. MacRoberts 7825* (LSU).

CYPERACEAE

Carex arkansana (L.H. Bailey) L.H. Bailey—Louisiana is not included in the range of *Carex arkansana* by Ball (2002) but is so included by Kartesz and Meacham (2005), USDA, NRCS (2007), NatureServe (2007), and Thomas and Allen (1993). MacRoberts (1989) and Thomas and Allen (1993) cite a specimen from Caddo Parish (*Thieret 25936* – LAF) collected in 1967 as the only record for Louisiana. B.R. MacRoberts and M.H. MacRoberts (2006) examined this specimen and confirmed its identification. On 2 May 2006, the authors discovered a small population of *C. arkansana* growing in a depression in a saline prairie in De Soto Parish. On 4 May 2007, we found a much larger population in a wet swale in a different part of the same prairie complex, adjacent to *Quercus similis-Crataegus brachyacantha* flatwoods. Our record is only the second record for this species in Louisiana and came 40 years after Thieret first collected it from the state.

Voucher specimen: **De Soto Parish:** Dickson Prairie, S side of Cypress Bayou, 2 air mi NE of Stonewall, NW1/4 S9 T15N R14W, rare, tiny depression in saline prairie, associated with *Carex* (*vulpinoidea*?), full sun, 2 May 2006, *Reid 5748, Faulkner et al.* (LSU, SWSL)

POACEAE

Panicum diffusum Sw.—On 20 June 2007 we found *Panicum diffusum* to be locally common in a saline prairie remnant in Sabine Parish. It was associated with open slicks with much bare soil and light vegetative cover. This record is apparently the first for Louisiana as the species is not reported for the state by NatureServe (2007), USDA, NRCS (2007), Thomas and Allen (1993), Allen et al. (2004), nor Freckman and Lelong (2003). *Panicum diffusum* was previously known in the United States only from Texas; its range extends south to the Caribbean and Latin America (Diggs et al. 2006; Freckman & Lelong 2003).

Voucher specimen: **Sabine Parish:** Oakley's Pasture (a.k.a. Mary Lee's Pasture), N of LA 174 ca. 5 mi W of Converse, along E side of McDonald Bayou, NW1/4 NW1/4 S12 & SW1/4 SW1/4 S1, T9N R14W. lat/long: 314711N, 934544W, common in slicks in saline prairie, most of prairie converted to Bahia grass pasture except for these more extreme areas, *Talinum parviflorum & Sporobolus pyramidatus* common and characteristic, 20 Jun 2007, *Reid 6173, Faulkner et al.* (Ft. Polk Herbarium, LSU)

ACKNOWLEDGMENTS

We thank George Dickson and Ralph and Becky Dalton for allowing our surveys on Dickson and Dalton saline prairies, respectively. Sidney Evans and James Taylor allowed us to survey Barron Road Prairie in Caddo Parish. Judy Oakley allowed our survey of Oakley's Pasture. We thank Tommy Smith of Red River Forest Management for taking us to Rambin Bayou Prairie in De Soto Parish. Red River Forest Management also owns part of the *Grindelia lanceolata* population in Sabine Parish and we appreciate their kind permission to botanize on their lands. Robert Love of Louisiana Department of Wildlife and Fisheries informed us about Oakley's Pasture and an additional saline prairie site in Sabine Parish and led us to these sites. We thank D.W. and Patricia Little for allowing access to their property in order to collect *Senecio ampullaceus*. Ryan Hook allowed access to the *Senecio ampullaceus* location through his family's property and we appreciate his kindness and interest. Jason Singhurst verified our first collection of *Lechea san-sabeana*. We thank

Charles Bryson for verifying a duplicate of *Carex arkansana* and Robert Haynes for verifying a duplicate of *Sagittaria subulata*. Charles Allen verified a duplicate of *Panicum diffusum* and we appreciate his help. Dennis Bell made one last search at NLU for the Bossier Parish specimen of *Arabis canadensis* and we appreciate his help with trying to track down that specimen. We thank J. Scott Peterson, R. Dale Thomas, and an anonymous reviewer for providing helpful comments on this manuscript.

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BOOK NOTICE

Douglas J. Futuyma, H. Bradley Shaffer, and Daniel Simberloff (eds). 2007. **Annual Review of Ecology, Evolution, and Systematics: Volume 38, 2007.** (ISBN 978-0-8243-1438-5, hbk; ISSN 1543-592X). Annual Reviews Inc., 4139 El Camino Way, P.O. Box 10139, Palo Alto, California 94303-0139, U.S.A. (**Orders:** www.annualreviews.org, science@annualreviews.org, 1-800-523-8635, 1-650-493-4400, 1-650-424-0910 fax). $80.00 indiv., $197.00 inst. (USA), 876 pp., indexes, 7 5/8" × 9 3/8".

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SILENE FLOS-CUCULI SSP. *FLOS-CUCULI* (CARYOPHYLLACEAE) AND *EUPHORBIA PEPLUS* (EUPHORBIACEAE) NEW TO NORTH CAROLINA

Derick B. Poindexter

Appalachian State University
Biology Department
Boone, North Carolina 28608, U.S.A
poindexterdb@appstate.edu

ABSTRACT

Two taxa previously undocumented for the vascular flora of North Carolina are here reported. Both state records are from mountainous counties located in extreme northwestern North Carolina, in the Blue Ridge Physiographic Province of the Southern Appalachians. *Silene flos-cuculi* ssp. *flos-cuculi* is a European exotic that primarily occurs in the northeastern United States. This taxon was collected from a ruderal, old-field site in southeastern Alleghany County. The Eurasian exotic *Euphorbia peplus* has been documented in several adjacent states and is distributed throughout North America. This synanthropic species was observed in areas of heavy disturbance in central Watauga County.

RESUMEN

Dos taxones nunca antes documentados para la flora vascular de Carolina del Norte son aquí reportados. Ambos reportes estatales son de condados montañosos localizados en el extremo noroeste de Carolina del Norte, en la provincia fisiográfica Blue Ridge (Borde Azul) de los Apalaches del sur. *Silene flos-cuculi* ssp. *flos-cuculi* es una especie europea exótica que ocurre principalmente en el noreste de los Estados Unidos. Este taxon fue colectado en un viejo campo ruderal en el sureste del condado Alleghany. La especie Euroasiática exótica *Euphorbia peplus* ha sido documentada en varios estados adyacentes y se distribuye por toda Norteamérica. Esta especie sinantrópica fue observada en áreas seriamente perturbadas en el centro del condado de Watauga.

Silene flos-cuculi (L.) Clairv. ssp. **flos-cuculi** (syn. *Lychnis flos-cuculi* L.), Ragged Robin, is a showy introduced taxon in the Caryophyllaceae with deeply dissected, pink petals. This perennial European native is presumed to be established in the northeastern United States (Weakley 2007), but has also been reported in several other U.S. localities, including fifteen states and the District of Columbia. States with records of this plant are Connecticut, Maine, Maryland, Massachusetts, Montana, New Hampshire, New Jersey, New York, Ohio, Pennsylvania, Rhode Island, Vermont, Virginia, Washington, and Wisconsin (USDA, NRCS 2007). *Silene flos-cuculi* ssp. *flos-cuculi* was rare in abundance, with approximately four individuals observed in an old-field across from Rich Hill Church in the rural Glade Valley community. Associated taxa include *Dactylis glomerata* L., *Pinus virginiana* Mill., *Pteridium aquilinum* (L.) Kuhn var. *latiusculum* (Desv.) Underw. ex A. Heller, *Rubus argutus* Link, and *Sassafras albidum* (Nutt.) Nees. The four-lobed, lacerate petal morphology and pink coloration differs substantially from other *Silene* spp. in North Carolina.

Voucher specimens: **NORTH CAROLINA. Alleghany Co.:** Glade Valley, Rich Hill Church, at the jct. of Shawtown Rd. and Rich Hill Rd., at latitude 36°28'20" N and longitude 80'59'31" W, 18 May 2007, *Poindexter 07-136* (BOON, NCU).

Euphorbia peplus L., Petty Spurge, is an exotic annual in the Euphorbiaceae. This Eurasian introduced taxon has a transcontinental distribution in the United States, occurring in total of thirty-five states, including Hawaii and Alaska (USDA, NRCS 2007). This herbaceous species exhibits short fleshy stems, primarily alternate, obovate leaves, and a characteristic seed morphology of outer pitted faces and inner furrows. This plant was discovered to be frequent in ruderal communities created by regular human perturbation on the campus of Appalachian State University. An estimated 50–100 individuals were observed. Associated taxa include *Chamaesyce maculata* (L.) Small, *Ranunculus repens* L., *Cyperus strigosus* L., *Sonchus asper* (L.) Hill, *Senecio vulgaris* L., *Portulaca oleracea* L., and *Galinsoga quadriradiata* Ruiz & Pav.

Voucher specimens: **NORTH CAROLINA. Watauga Co.:** Boone; Appalachian State University, growing on campus grounds adjacent

to Rankin Science Bldg., parallel to Rivers St., in disturbed areas and permanent flower beds, at latitude 36°12'49" N and longitude 81°40'49" W, 15 Jun 2007, *Poindexter 07-205* (BEREA, BOON, NCU).

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ANNOTATED CHECKLIST OF THE VASCULAR FLORA OF THE BEECH CREEK UNIT OF THE BIG THICKET NATIONAL PRESERVE, TYLER COUNTY, TEXAS

Larry E. Brown

Herbarium, Spring Branch Science Center
8856 Westview Drive
Houston, Texas 77055, U.S.A.
larry-theplantman@att.net

Barbara R. MacRoberts and Michael H. MacRoberts

Bog Research, 740 Columbia
Shreveport, Louisiana 71104, U.S.A.
and Herbarium, Museum of Life Sciences
Louisiana State University in Shreveport
Shreveport, Louisiana, 71115, U.S.A.

Paul A. Harcombe, Warren W. Pruess, and I. Sandra Elsik

Department of Ecology and Evolutionary Biology
Rice University
Houston, Texas 77005, U.S.A.

Suzanne Birmingham Walker

Azimuth Forestry Services, Inc.
14671 State Highway 87 South
Shelbyville, Texas 75973. U.S.A.

ABSTRACT

An annotated, vouchered checklist is provided for the vascular plant taxa of the 2,059 hectare Beech Creek Unit, Big Thicket National Preserve, Tyler County, southeastern Texas. Documented in the unit are 470 taxa of which 52 taxa (11%) are exotics.

RESUMEN

Se aporta un catálogo con anotaciones y testigos de los taxa de plantas vasculares de las 2,059 hectáreas de la unidad Beech Creek, Big Thicket National Preserve, Tyler County, sureste de Texas. Los taxa documentados en la unidad son 470 de los que 52 (11%) son exóticos.

INTRODUCTION

This manuscript is the 5th part of an intended inventory, based on voucher specimens, of the vascular flora of the Big Thicket National Preserve, southeastern Texas. In 4 previous papers, we provided an annotated checklist of the Hickory Creek, Turkey Creek, Big Sandy Creek, and Lance Rosier units (MacRoberts et al. 2002; Brown et al. 2005, 2006a, 2006b). In this paper, we provide an annotated checklist of the Beech Creek Unit.

SITE AND METHODS

The Big Thicket is located mostly within the longleaf pine region of the West Gulf Coastal Plain in southeastern Texas (Ajilvsgi 1979; Harcombe & Marks 1979; Watson 1979; Marks & Harcombe 1981; Harcombe et al. 1993; Diggs et al. 2006 and references therein). The Big Thicket National Preserve consists of 12 units scattered over 7 Texas counties. The units range from 222 to 10,100 hectares and total about 34,000 hectares (Peacock 1994). The Beech Creek Unit consists of 2,059 hectares and is located in western Tyler County (Fig. 1). It is relatively flat with poor drainage over most of the area. Elevation ranges from about 43 meters to 62 meters. Little Beech Creek and Beech Creek run through the unit. The Beech Creek Unit was chosen for inclusion in the Big Thicket National Preserve because of its extensive stands of beech forest (Ajilvsgi 1979; Harcombe & Marks 1979; Watson 1979; Marks & Harcombe 1981). It is dominated by lower slope hardwood-pine forest (mesic lower slopes and terraces), with lesser amounts of baygall, mid-slope oak-pine forest, floodplain hardwood-pine forest (mesic stream bottoms), and floodplain hardwood forest (seasonally flooded river floodplain) (Harcombe & Marks 1979; Marks & Harcombe 1981; Van Kley 2006). A map of community types can be found in Harcombe and Marks (1979). Fire suppression over the past 30 years has resulted in extensive midstory development and thus reduction of herbaceous vegetation that

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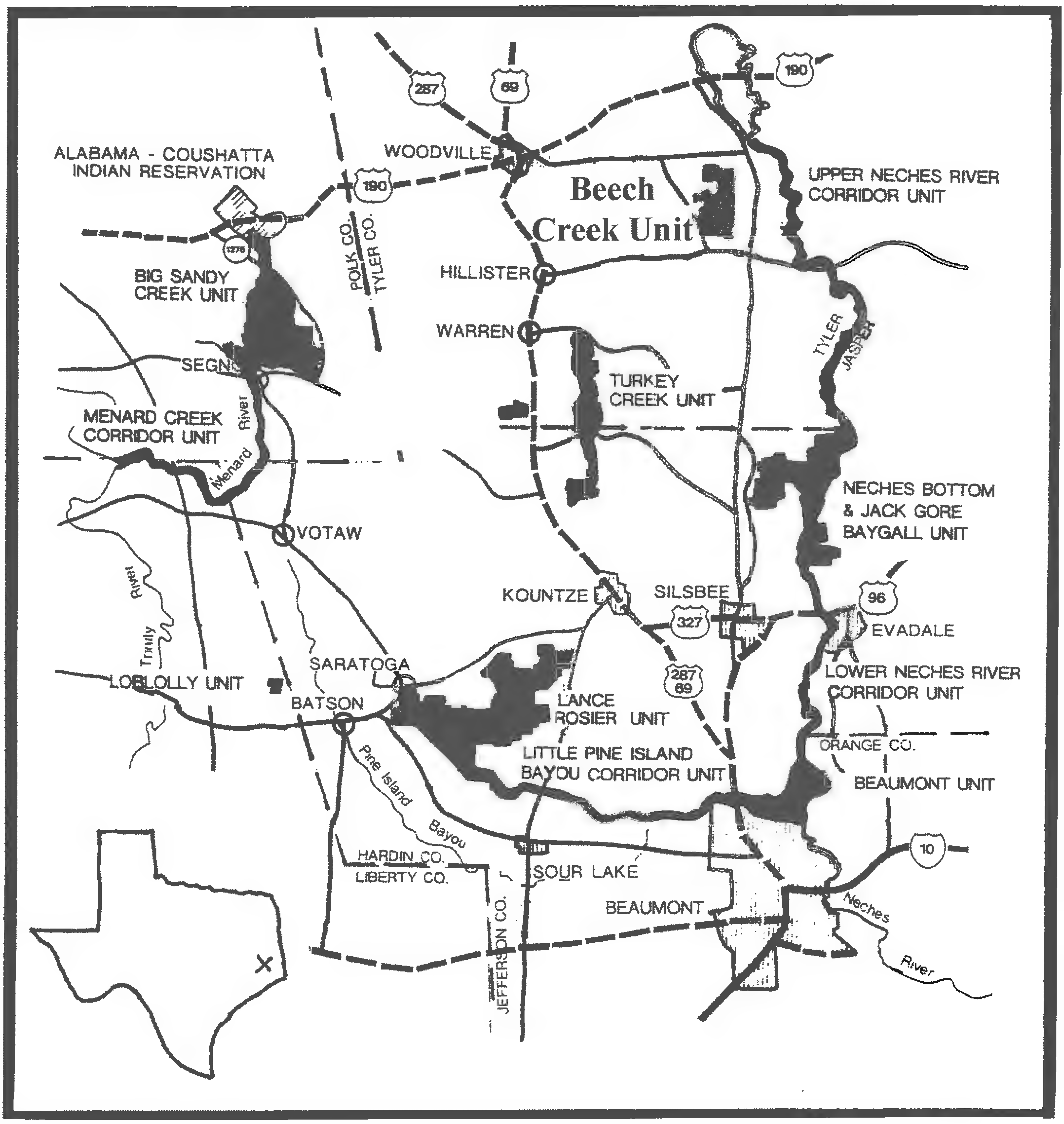

Fig. 1. Location of the Beech Creek Unit, Big Thicket National Preserve, Texas.

is adapted to frequent fires. Hurricane Rita, a category 3 hurricane, passed over the unit on 24 September 2005 damaging and toppling thousands of trees. It will probably take decades for this litter to decompose. Details about soils, topography, and climate can be found in Deshotels (1978); Watson (1979, 1982, 2006); Harcombe and Marks (1979); Marks and Harcombe (1981); and Diggs et al. (2006).

Like most units of the Big Thicket National Preserve, the Beech Creek Unit has not been the subject of a detailed floristic inventory.

Larry Brown collected 290 specimens during 9 field days beginning 9 November 2006 and ending 17 October 2007. The MacRobertses collected 154 specimens during 4 field days in 2004 and 1 day in 2007. Suzanne Walker collected 101 specimens during 2 days in 2004 and 1 additional day in 2007. Sandi Elsik and Warren Pruess together gathered 82 specimens during 2005. Geraldine Watson collected 25 specimens

over several years in the late 1970s and early 1980s. Warren Pruess collected another 11 specimens over a 2 year period. Other collectors totaled 12 specimens. We conducted a search of the Texas A&M University (TAMU) herbarium consortium data base (http://www.csdl.tamu.edu/FLORA/tracy/main/html/) for additional specimens but found no additional taxa not reported here.

Because our purpose was to produce a list of taxa known to occur on the Beech Creek Unit, a vouchered specimen was considered to be the only evidence acceptable for inclusion in the list. In all, 675 herbarium specimens form the data for this report. All specimens have been annotated by Larry Brown.

In most cases, nomenclature follows Jones et al. (1997), Kartesz (1999), Turner et al. (2003), and Diggs et al. (2006). In cases of multiple collections, no more than 4 are listed for each taxon.

RESULTS

The following is an annotated list of the Beech Creek Unit taxa. Abbreviations used are given below.

GW = Geraldine Watson. Her collections are at TAES.
JL = Joe Liggio. His collections are at TAES.
LB = Larry Brown. His specimens are at TAES.
MM = Barbara and Michael MacRoberts. Their specimens are at TAES.
PH = Paul Harcombe. His collections are at TAES.
PM = Phil Malnassey. His collections are at TAES.
RH = Roland Harper (grandson of LB).
SEWP = Sandra Elsik and Warren Pruess. Their specimens are at TAES.
SH = Shawn Harper (grandson of LB).
SW = Suzanne Walker. Her specimens are at TAES.
WP = Warren Pruess. His specimens are at TAES.
WRC = Bill Carr. His collections are at TEX/LL.
* = exotic
\+ = see note at end of list.

Acanthaceae
Justicia ovata (Walter) Lindau var. *lanceolata* (Chapm.) R.W. Long, SW 67, 46
Ruellia caroliniensis (J.F. Gmel.) Steud., SEWPLB 488; LBSH 32151
Ruellia humilis Nutt., MM 7150

Aceraceae
Acer rubrum L., MM 7078

Agavaceae
**Yucca aloifolia* L., LB 31939; SEWP 272
Yucca louisianensis Trel., MM 7141

Anacardiaceae
Rhus copallinum L., SEWP 249
Toxicodendron radicans (L.) Kuntze, SEWP 337; LB 32783
Toxicodendron vernix (L.) Kuntze, SEWP 341

Annonaceae
Asimina parviflora (Michx.) Dunal, SW 03; LB 31996, 32178; MM 7097

Apiaceae
Centella erecta (L.f.) Fernald, SW 03
Chaerophyllum tainturieri Hook. var. *tainturieri*, WP 113
Cicuta maculata L., SEWP 414
**Cyclospermum leptophyllum* (Pers.) Sprague ex Britton & P. Wilson, SW 58
Eryngium prostratum Nutt. ex DC., SW 68
Hydrocotyle verticillata Thunb., SEWP 262; LB 32783
Ptilimnium capillaceum (Michx.) Raf., LB 31994; LBSH 32122
Sanicula canadensis L., SW 71
Sanicula smallii E.P. Bicknell, WP 111

Apocynaceae
Trachelospermum difforme (Walter) A. Gray, LB 31998

Aquifoliaceae
Ilex ambigua (Michx.) Torr., PH 001
Ilex coriacea (Pursh) Chapm., SW 012
Ilex longipes Chapm. ex Trel., PH 002
Ilex opaca Aiton, MM 7056
Ilex vomitoria Sol. in Aiton, MM 7058

Araceae
Arisaema triphyllum (L.) Schott, SW 10, 31

Araliaceae
Aralia spinosa L., SEWP 245

Arecaceae
Sabal minor (Jacq.) Pers., MM 7131

Aristolochiaceae
Aristolochia serpentaria L., SW 05; GW 2261

Asclepiadaceae
Asclepias perennis Walter, SEWP 230
Asclepias variegata L., LBRH 32061

Aspleniaceae
Asplenium platyneuron (L.) Britton, Sterns, & Poggenb., WP 116

Asteraceae
Ambrosia artemisiifolia L., MM 7198
Ambrosia trifida L., SEWP 265
Baccharis halimifolia L., LBRH 32071; SW 105
Bidens aristosa (Michx.) Briton, LB 33034
Bidens bipinnata L., SEWP 252; LB 33030
Bidens frondosa L., LB 33003
Boltonia diffusa Ell., MM 7199
+*Bradburia pilosa* (Nutt.) Semple, SEWPLB 491, 501; MM 7197
Cirsium horridulum Michx., SEWP 240; SW 111
Conoclinium coelestinum (L.) DC., SW 44b; LB 33039
Conyza bonariensis (L.) Cronquist, LB 32466
Conyza canadensis (L.) Cronquist, SEWP 335; LBJL 32616a
Coreopsis lanceolata L., SW 063
Coreopsis tinctoria Nutt., SEWP 253

Elephantopus carolinianus Raeusch., SW 74; LBJL 32959
Elephantopus nudatus A. Gray, LB 33002
Elephantopus tomentosus L., LB 28598a, 28353; SEWP 327; LBJL 32616
Erechtites hieraciifolia (L.) Raf. ex DC., SEWP 342
Erigeron strigosus Muhl. ex Willd., MM 7139; LBRH 32060
Eupatorium capillifolium (Small) Lam., PM 03; LB 32457
Eupatorium lancifolium (Torr. & A. Gray) Small, LBSEWP 31899; MM 7187
Eupatorium mohrii Greene, SEWPLB 496
Eupatorium perfoliatum L., SW 83; MM 7147
Eupatorium x pinnatifidum Elliott, LB 33004
Eupatorium rotundifolium L., SW 39a; LB 33039
Eupatorium semiserratum DC., LB 32491
Eupatorium serotinum Michx., SW 43; PM 02; LB 33016
Euthamia leptocephala (Torr. & A. Gray) Greene ex Porter & Britton, LBSEWP 31894
**Facelis retusa* (Lam.) Sch. Bip., LBRH 32048; MM 7683
Gaillardia pulchella Foug.. var. *pulchella*, SEWP 255
Gamochaeta coarctata (Willd.) Kerguelen, MM 7106
Gamochaeta purpurea (L.) Cabrera, SW 061
Helenium amarum (Raf.) H. Rock var. *amarum*, MM 7135
Helianthus angustifolium L., SEWP 403b; LB 33023
Hieracium gronovii L., LB 32494
Hymenopappus artemisiifolius DC. var. *artemisiifolius*, MM 7148
**Hypochaeris microcephala* (Sch. Bip.) Cabrera var. *albiflora* (Kuntze) Cabrera, LBRH 32075; MM 7661
Krigia cespitosa (Raf.) Chambers, LB 32001; LBRH 32051
Krigia virginica (L.) Willd., MM 7678
Mikania scandens (L.) Willd., SW 33, 86
Lactuca canadensis L., LB 32166
Pluchea camphorata (L.) DC., MM 7211, 7212; LB 32804
Pluchea foetida (L.) DC., MM 7236; SW 92
Pyrrhopappus carolinianus (Nutt.) Wooten & Standl., LB 32462
Pyrrhopappus pauciflorus (D. Don) DC., WP 119; SW 125
Rudbeckia hirta L., MM 7112; LBRH 32074
Solidago altissima L., SW 100; LB 33015
Solidago ludoviciana (A. Gray) Small, SEWPLB 502
Solidago rugosa Mill. var. *aspera* (Aiton) Fernald, LBSEWP 31887; SEWP 331; LB 33024
**Sonchus asper* (L.) Hill, LB 32006; SEWP 544; SW 113
Symphyotrichum dumosum (L.) G.L. Nesom, MM 7206
Symphyotrichum lateriflorum (L.) A. & D. Love, WP 120; MM 7668; GW 2248; SEWPLB 481
Symphyotrichum racemosum (Elliott) G.L. Nesom, LBSEWP 31886; LB 33001

Berberidaceae
Podophyllum peltatum L., MM 7109

Betulaceae
Alnus serrulata (Aiton) Willd., GW 2250
Betula nigra L., SEWP 360
Carpinus caroliniana Walter, MM 7083
Ostrya virginiana (Mill.) K. Koch, MM 7126

Bignoniaceae
Bignonia capreolata L., MM 7065
Campsis radicans (L.) Seem. ex Bureau, SW 02, 49

Blechnaceae
Woodwardia areolata (L.) T. Moore, SW 47; MM 7659
Woodwardia virginica (L.) Small, MM 7238; LB 33036

Brassicaceae
**Cardamine hirsuta* L., LB 31943
Cardamine parviflora L. var. *arenicola* (Britt.) Schultz, LB 31942

Bromeliaceae
Tillandsia usneoides (L.) L., SEWP 395

Buddlejaceae
Polypremum procumbens L., PM 04; LBJL 32601

Burmanniaceae
Apteria aphylla Barnhart., MM 7224; SW 88; LB 33009
Burmannia biflora L., SEWP 422

Callitrichaceae
Callitriche peploides Nutt., LB 32017

Campanulaceae
Lobelia cardinalis L., SW 84; MM 7209
Lobelia appendiculata A. DC., MM 7673; LBSH 32149
Lobelia puberula Michx., SW 34; GW 2249, 2336; LB 31934
Triodanis biflora (Ruiz & Pavon) Greene, LB 32009; LBRH 32059; MM 7674
Triodanis perfoliata (L.) Nieuwl. LBRH 32059
**Wahlenbergia marginata* (Thunb.) A. DC., WP 121; LB 32487; SW 110

Caprifoliaceae
**Lonicera japonica* Thunb., MM 7162
Sambucus nigra L. subsp. *canadensis* (L.) R. Bolli, SW 60, BT050
Viburnum acerifolium L., SW 57
Viburnum dentatum L., SW 48
Viburnum nudum L. var. *nudum*, GW 2260b; LB 32170

Celastraceae
Euonymus americanus L., SEWP 418

Cistaceae
Lechea mucronata Raf., GW 06b; PM 06
Lechea tenuifolia Michx., LBRH 32058

Clethraceae
Clethra alnifolia L., SW 20; MM 7119

Commelinaceae
Commelina erecta L., LBSH 32126
Commelina virginica L, MM 7155; LBSH 32120

Convolvulaceae
Dichondra carolinensis Michx., MM 7161
Ipomoea cordatotriloba Dennst var. *cordatotriloba*, SEWP 350; LB 33031
Ipomoea pandurata (L.) G. Mey., LB 32493
Jacquemontia tamnifolia (L.) Griseb., SEWPLB 500

Cornaceae
Cornus florida L., MM 7087
Nyssa aquatica L., SEWP 362
Nyssa biflora Walter, SEWP 397
Nyssa sylvatica Marsh., SEWP 275; MM 7081

Crassulaceae
Penthorum sedoides L., LB 32805

Cupressaceae
Juniperus virginiana L. var. *virginiana,* MM 7076; LB 33032
Taxodium distichum (L.) L.C. Rich., SW 42

Cucurbitaceae
**Citrullus lanatus* (Thunb.) Matsum & Nakai LB 33011

Cuscutaceae
Cuscuta compacta Juss. ex Choisy, MM 7231; LB 33007

Cyperaceae
Carex albicans Willd. ex Spreng. var. *australis* (L.H. Bailey) Rettig, LB 31936
Carex brevior (Dewey) Mack. ex Lunell, SW 127
Carex cherokeensis Schwein., LB 32004
Carex complanata Torr. & Hook., LB 31953, 31989; MM 7677
Carex corrugata Fernald, LB 32016
Carex debilis Michx. var. *debilis*, MM 7231
Carex digitalis Schkuhr ex Willd. var. *floridana* (L.H. Bailey) Naczi & Bryson, LB 31947, 32007; LBSH 32133; MM 7672
Carex flaccosperma Dewey, LB 32014, 32015
Carex frankii Kunth, LB 32175
Carex glaucescens Elliott, MM 7210; LBJL 32600
Carex intumescens Rudge, LBRH 32046; MM 7663; SW 129; LB 32065
Carex joorii L.H. Bailey, SEWP 351
Carex leptalea Wahlenb subsp. *harperi* (Fernald) W. Stone, LBSEWP 31889; LB 32023
Carex lurida Wahlenb., LBSH 32148; LBJL 32618; SW 119
+*Carex* section *ovales*, LB 31987
Cyperus croceus Vahl, LBRH 32067
**Cyperus entrerianus* Boeck., SEWPLB 503
Cyperus erythrorhizos Muhl., LB 32794
Cyperus haspan L., SEWP 356; LB 32481
Cyperus odoratus L., SEWP 400
Cyperus pseudovegetus Steud., LB 32165
Cyperus virens Michx., MM 7666
Eleocharis microcarpa Torr., LBSH 32134a
Eleocharis tuberculosa (Michx.) Roem. & Schult., LBSEWP 31895; MM 7233; LBRH 32047; MM 7662
Kyllinga odorata Vahl, LB 32484
Kyllinga pumila Michx., SEWP 399
Rhynchospora caduca Elliott, MM 7127; LBSH 32150
Rhynchospora corniculata (Lam.) A. Gray, SEWP 231
+*Rhynchospora debilis* Gale, LBSH 32140; LBRH 32087
Rhynchospora elliottii A. Dietr., LBSH 32214
Rhynchospora fascicularis (Michx.) Vahl, LB 32479
Rhynchospora globularis (Chapm.) Small var. *globularis* LBSH 32132, 32220
Rhynchospora glomerata (L.) Vahl, SW 98; LB 32472, 33019
Rhynchospora inexpansa (Michx.) Vahl, MM 7118
Rhynchospora mixta Britton, MM 7074; LB 33038
Rhynchospora plumosa Elliott, LB 32022; LBRH 32078; MM 7676; SW 109
Rhynchospora pusilla Chapm. ex M.A. Curtis, LBSH 3214
Scirpus cyperinus L., LB 32164
Scleria oligantha Michx., LB 31995; MM 7671
Scleria triglomerata Michx., MM 7192; LB 32019; LBJL 32593; SW 120

Cyrillaceae
Cyrilla racemiflora L., SW 22; MM 7121

Dennstaedtiaceae
Pteridium aquilinum (L.) Kuhn, SW 96; MM 7133

Dioscoreaceae
Dioscorea villosa L., GW 2288

Droseraceae
Drosera brevifolia Pursh, SW 27; MM 7654

Dryopteridaceae
Athyrium filix-femina (L.) Roth var. *asplenioides* (Michx.) Farw., MM 7153
Onoclea sensibilis L., MM 7228; LBSH 32127
Polystichum acrostichoides (Michx.) Schott, LB 31937

Ebenaceae
Diospyros virginiana L., LB 32482

Ericaceae
Leucothoe racemosa (L.) A. Gray, SEWP 359
Lyonia ligustrina (L.) DC., MM 7123
Lyonia mariana (L.) D. Don, SEWP 416
Monotropa uniflora L., SW 89; MM 7117; LB 33035
Rhododendron canescens (Michx.) Sweet, WP 112
Rhododendron viscosum (L.) Torr., SW 18; MM 7122; LBSH 32129
Vaccinium arboreum Marshall, PH 005
Vaccinium corymbosum L., SW 19, 130, 45; LB 31950

Euphorbiaceae
Acalypha gracilens A. Gray, SW 99; GW 2255
Chamaesyce maculata (L.) Small, SEWP 247
Chamaesyce nutans (Lag.) Small, SEWP 251
Croton capitatus Michx., MM 7200
Croton glandulosus L. var. *septentrionalis* Muell.-Arg., SEWP 270
Croton monanthogynus Michx., SEWP 259
Croton willdenowii G.L. Webster, LB 32490
Euphorbia corollata L., LB 32807
Euphorbia dentata Michx., SEWP 254; LB 32460
Phyllanthus caroliniensis Walter, LB 32475
**Phyllanthus urinaria* L., MM 7111
Sebastiania fruticosa (W. Bartram) Fernald, SW 14
**Triadica sebifera* (L.) Small, SW 01

Fabaceae
**Albizia julibrissin* Durazz., MM 7107
Centrosema virginianum (L.) Benth, LBJH 32604
Cercis canadensis L. var. *canadensis*, SEWP 271
Chamaecrista fasciculata (Michx.) Greene, SEWP 276; LBJL 32605
Chamaecrista nictitans (L.) Moench, LB 32461, 32179, 32486, 32806
Crotalaria sagittalis L., SW 65; LB 32488
Desmodium ciliare (Muhl. ex Willd.) DC., SEWPLB 497
Desmodium glabellum (Michx.) DC., GW 2337
Desmodium paniculatum DC., MM 7189
Erythrina herbacea L., SEWP 4121
Galactia volubilis (L.) Britton, LB 32489
Glottidium vesicarium (Jacq.) Harper, SEWP 43
**Kummerowia striata* (Thumb.) Schlindler, LBSH 32128

Lespedeza cuneata (Dum-Cours.) Harper, SEWP 348
Lespedeza virginica (L.) Britton, LB 32808
**Medicago lupulina* L., LB 31941
Mimosa hystricina (Small ex Britton & Rose) B.L. Turner, LBSH 32119
Rhynchosia latifolia Nutt., LBRH 32050
Strophostyles umbellata (Muhl. ex Willd.) Britton, SEWP 347; LBSH 32118; LB 32809
Stylosanthes biflora (L.) Britton, Sterns, & Poggenb., SEWP 235
**Trifolium campestre* Schreb., MM 7151; LBSH 32152
**Trifolium incarnatum* L., SW 124
**Trifolium lappaceum* L., LB 32172
Wisteria frutescens (L.) Poir., LB 31999
**Wisteria sinensis* (Sims) Sweet, SW 131
**Vicia sativa* L. subsp. *nigra* (L.) Ehrhart, LB 32002; MM 7665

Fagaceae
Castanea pumila (L.) Mill., SEWP 408; LB 33021
Fagus grandifolia Ehrh., SW 09; MM 7075
Quercus alba L., SW 06; MM 7077
Quercus falcata Michx., SW 52; MM 7108
Quercus hemisphaerica Bartr. ex Willd., SW 54, 55; LB 33028; MM 7089
Quercus laurifolia Michx., SEWP 344
Quercus margaretta Ashe ex Small, SEWP 424
Quercus michauxii Nutt., MM 7229; SW 44a
Quercus nigra L., MM 7085
Quercus phellos L., SEWPLB 484
Quercus velutina Lam., LBRH 32084

Gentianaceae
+*Bartonia texana* Correll, SEWP 340; LB 33010
**Centaurium pulchellum* (Sw.) Druce, SW 108
Sabatia campestris Nutt., LB 32169

Geraniaceae
Geranium carolinianum L., WP 118

Grossulariaceae
Itea virginica L., SEWP 403a; LB 32024, 32784; MM 7660

Haloragaceae
Proserpinaca palustris L., SEWPLB 489

Hammamelidaceae
Hamamelis vernalis Sarg., MM 7054
Hamamelis virginiana L., MM 7217; GW 2289
Liquidambar styraciflua L., MM 7053

Hypericaceae
Hypericum drummondii (Grev. & Hook.) Torr. & A. Gray, GW 2259; LBJL 32617
Hypericum galioides Lam., MM 7207; GW 2257
Hypericum gentianoides (L.) Britton, Sterns, & Poggenb., LB-SEWP 31896; SW 95
Hypericum hypericoides (L.) Crantz, SW 73; MM 7220; LBRH 32063; LBJL 32599
Hypericum mutilum L., SW 66, 25
Triadenum walteri (J.G. Gmel.) Gleason, SW 35, 85

Iridaceae
Sisyrinchium campestre E.P. Bicknell, SEWP 543
Sisyrinchium sagittiferum E.P. Bicknell, LB 31952
Sisyrinchium rosulatum E.P. Bicknell, LB 32011; MM 7684, 7680; SW 114

Juglandaceae
Carya aquatica (Michx. f.) Nutt., SEWPLB 495
Carya texana Buckley, SEWP 412
Carya tomentosa (Lam. ex Poir.) Nutt., SW 28

Juncaceae
Juncus acuminatus Michx., LB 32005; LBRH 32069; LBSH 32142a
Juncus anthelatus (Wiegand) R.L. Brooks, LB 31997
Juncus coriaceus Mack., SW 40
Juncus diffusissimus Buckley, LBRH 32070, 32077; LBSH 32123; LB 32473
Juncus effusus L., LB 31938
Juncus marginatus Rostk, MM 7130; LBRH 32049
Juncus repens Michx., SEWP 355
Juncus scirpoides Lam., LB 32799
Juncus tenuis Willd., LB 32020
Juncus validus Coville, MM 7167; LBRH 32088
Luzula bulbosa (A.W. Wood) Smyth, LB 31935

Lamiaceae
Hyptis alata (Raf.) Shinners, SEWP 404
Lycopus rubellus Moench, SEWP 398
Lycopus virginicus L., MM 7227; SW 80; LB 32797
Monarda citriodora Cerv. ex Lag., MM 7203
Monarda punctata L. var. *punctata*, LB 32492
**Perilla frutescens* (L.) Britton, SEWP 267
Prunella vulgaris L., MM 7160
Pycnanthemum albescens Torr. & A. Gray, SEWPLB 499
Pycnanthemum tenuifolium Schrad., LB 32176
Salvia lyrata L., MM 7096
Scutellaria elliptica Muhl. ex Spreng., SEWP 239; LB 32013
Scutellaria integrifolia L., LBRH 32043
Stachys crenata Raf., LB 32008
Teucrium cubense Jacq., SW 69; MM 7157
Trichostema dichotomum L., SW 77; LB 33020

Lauraceae
Persea borbonia (L.) Spreng., SW 08, MM 7088
Persea palustris (Raf.) Sarg., SEWPLB 480; LB 32785
Sassafras albidum (Nutt.) Nees, SEWP 241

Liliaceae
Hypoxis curtissii Rose, SW 39, 97, 82; LBJL 32594
Lilium michauxii Poir., LBSH 32136
Nothoscordum bivalve (L.) Britton, MM 7216; LB 33022

Linaceae
Linum medium (Planch.) Britton var. *texanum* (Planch.) Fernald, MM 7142
Linum striatum Walter, MM 7174; LBSH 32146

Loganiaceae
Gelsemium sempervirens (L.) Aiton f., SW 07; MM 7067; LB 33008
Mitreola petiolata (J.F. Gmel.) Torr. & A. Gray, SW 75; LB 32802

Lygodiaceae
**Lygodium japonicum* (Thunb. ex Murray) Sw., SW 87; MM 7072

Lythraceae
**Cuphea carthagenensis* (Jacq.) J.F. Macbr., SW 30; WRC 11400

**Cuphea glutinosa* Cham. & Schlecht., LB 3246
Rotala ramosior (L.) Koehne, LB 32789

Magnoliaceae
Magnolia grandiflora L., MM 7061
Magnolia virginiana L., SW 15

Malvaceae
Sida rhombifolia L., MM 7171

Melastomataceae
Rhexia mariana L., MM 7149

Meliaceae
**Melia azedarach* L., SEWPLB 504

Moraceae
Maclura pomifera (Raf.) C.K. Schneid., GW 2296
Morus rubra L., SEWP 266; MM 7134

Myricaceae
Morella caroliniensis (Mill.) Small, SW 21; MM 7090; LBSH 32121
Morella cerifera (L.) Small, LB 32790

Oleaceae
Chionanthus virginicus L., SEWP 409
Fraxinus americana L., MM 7213, 7063; GW 2252; SW 113
Fraxinus caroliniana Mill., SEWP 361; LB 32786
Fraxinus pennsylvanica Marsh., LB 32795
**Ligustrum sinense* Lour., MM 7146

Onagraceae
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Ludwigia decurrens Walter, GW 2333; LB 32801
Ludwigia glandulosa Walter, SEWP 401
Ludwigia leptocarpa (Nutt.) Hara, SEWP 358
Ludwigia pilosa Walter, SEWP 406; LB 32796, 33017
Ludwigia palustris (L.) Elliott, LB 31993
Oenothera biennis L., SEWP 392
Oenothera laciniata Torr. & A. Gray, LBRH 32052; SW 106
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Ophioglossaceae
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Orchidaceae
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Spiranthes vernalis Engelm. & A. Gray, SW 121
Tipularia discolor (Pursh) Nutt., MM 7219, 7091; LBJL 32598

Orobanchaceae
Epifagus virginiana (L.) W. Bart., SW 90

Osmundaceae
Osmunda cinnamonea L., SW 23
Osmunda regalis L. var *spectabilis* (Willd.) A. Gray, SW 13

Oxalidaceae
Oxalis corniculata L.var. *wrightii* (A. Gray) Turner, MM 7095; LB 31951; SW 117
**Oxalis debilis* Kunth var. *corymbosa* (DC.) Lourteig, MM 7664

Passifloraceae
Passiflora lutea L., MM 7060

Phytolaccaceae
Phytolacca americana L., MM 7110

Pinaceae
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Pinus taeda L., MM 7093

Plantaginaceae
Plantago virginica L., MM 7094; LBRH 32079

Platanaceae
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**Aira caryophyllea* L. var. *capillaris* Mutel, LBRH 32054
Andropogon glomeratus (Walter) Britton, Sterns, & Poggenb., MM 7196
Andropogon virginicus L., SW 101
Aristida purpurascens Poir. var. *purpurascens*, MM 7191; LB 33037, 33041
Arundinaria gigantea (Walter) Muhl., MM 7172
Axonopus fissifolius (Raddi) Kuhlm., LBRH 32076
**Bothriochloa ischaemum* (L.) Keng var. *songarica* (Fish. & Mey) Celarier & Harlan, LB 33018
**Briza minor* L., SW 62; MM 7152
**Bromus catharticus* Vahl, LBRH 32072; MM 7658
Chasmanthium laxum (L.) H.O. Yates, MM 7104
Chasmanthium sessiliflorum (Poir.) H.O. Yates, SEWPLB 498
**Cynodon dactylon* (L.) Pers., SEWP 246
Dichanthelium aciculare (Desv. ex Poir.) Gould & C.A. Clark var. *aciculare*, LB 32459, 33000
Dichanthelium acuminatum (Sw.) Gould & C.A. Clark var. *acuminatum*, LBRH 32089; LBSH 32142
Dichanthelium boscii (L.) Gould & C.A. Clark, MM 7165; LB 31990, 32180
Dichanthelium commutatum (Schult.) Gould subsp. *commutatum* LBSEWP 31891; LB 31949
Dichanthelium dichotomum (L.) Gould subsp. *dichotomum*, SEWP 332; MM 7137, 7071; LBSH 32134
Dichanthelium dichotomum (L.) Gould subsp. *microcarpon* (Muhl. ex Elliott) Freckman & Lelong, LBRH 32083; LB 32171
Dichanthelium dichotomum (L.) Gould subsp. *roanokense* (Ashe) Freckman & Lelong, LBSH 32131
Dichanthelium laxiflorum (Lam.) Gould, LBSEWP 31890
Dichanthelium oligosanthes (Schult.) Gould var. *oligosanthes*, LB 32018, 32471; LBRH 32064
Dichanthelium polyanthes (Schult.) Mohlenbr., MM 7136
Dichanthelium scabriusculum (Elliott) Gould & C.A. Clark, LBRH 32086
Dichanthelium scoparium (Lam.) Gould, MM 7218; LB 33005
Dichanthelium tenue (Muhl.) Freckmann & Lelong, LBRH 32044; LBSH 32138, 32123a, 32121a
Digitaria ciliaris (Retz.) Koel., GW 2330; LB 32476, 32458
**Digitaria ischaemum* (Schreb.) Muhl., MM 7232
**Eleusine indica* (L.) Gaertn., SEWP 248
Elymus virginicus L., LB 32177
Eragrostis hirsuta (Michx.) Nees, LB 33040
Eragrostis refracta (Muhl.) Scribn., MM 7230
Eragrostis spectabilis (Pursh) Steud., LB 33025

Hordeum pusillum Nutt., LB 32010
Leersia virginica Willd., LBSEWP 31892; MM 7195
**Lolium perenne* L., LBRH 32073
Melica mutica Walter, MM 7168
Oplismenus hirtellus (L.) P. Beauv. subsp *setarius* (Lam.) Mez ex Ekman, SEWPLB 483
Panicum anceps Michx., LB 32485
Panicum brachyanthum Steud., MM 7201
Panicum rigidulum Bosc ex Nees, SEWP 396
Panicum verrucosum Muhl., MM 7193; WRC11402; LB 33006
**Paspalum dilatatum* Poir., LB 32463
Paspalum langei (E. Fourn.) Nash, SEWPLB 494
**Paspalum notatum* Fluegge, MM 7158
Paspalum plicatulum Michx., SW 64; MM 7190
Paspalum setaceum Michx., LB 32478
**Paspalum urvillei* Steud., MM 7202; SW 70; GW 2328
Phalaris caroliniana Walter, LBSH 32144
Piptochaetium avenaceum (L.) Parodi, LB 31992
**Poa annua* L., WP 117
**Sacciolepis indica* (L.) Chase, LBSEWP 31897; SW 04; WRC 11401
**Schedonorus arundinaceus* (Schreb.) Dumort., LB 32003
Schizachyrium scoparium (Michx.) Nash, LB 32803
Sphenopholis intermedia (Rydb.) Rydb., LB 31985; MM 7656
Sphenopholis obtusata (Michx.) Scribn., LBSH 32145
Sporobolus indicus (L.) R. Br., SW 102; GW 2329
Tridens flavus (L.) Hitchc. var. *flavus*, SW 103
Vulpia octoflora (Walter) Rydb., LBRH 32057

Polygalaceae
Polygala mariana Mill., LBJL 32615
Polygala polygama L., LBRH 32045

Polygonaceae
Brunnichia ovata (Walter) Shinners, SEWP 402a
Polygonum punctatum Elliott., SEWPLB 485
Rumex hastatulus Baldw., LBRH 32055

Polypodiaceae
Pleopeltis polypodioides Andrews & Windham subsp. *michauxiana* (Weatherby) Andrews & Windham, GW 53; MM 7105; SEWP 402b; SW 81

Primulaceae
**Anagallis arvensis* L., MM 7657
Samolus valerandi L. subsp. *parviflorus* (Raf.) Hulten, LBSEWP 31888

Rhamnaceae
Berchemia scandens (Hill) K. Koch, MM 7057
Frangula caroliniana (Walter) A. Gray, MM 7082; LB 33026

Rosaceae
Crataegus marshallii Egglest., MM 7156
Crataegus opaca Hook. & Arn. ex Hook., LBSH 32135
Crataegus spathulata Michx., MM 7166, 7064
**Duchesnea indica* (Andr.) Focke, MM 7215
Prunus caroliniana (Mill.) Aiton, MM 7068
Prunus serotina Ehrh., SEWP 426
Rubus argutus Link, SEWPLB 482
Rubus trivialis Michx., MM 7144

Rubiaceae
Cephalanthus occidentalis L., MM 7154
Diodia teres Walter, SEWP 234
Diodia virginiana L., SEWP 237
Galium pilosum Aiton, SEWPLB 492
Houstonia pusilla Schoepf., LB 31933
Mitchella repens L., MM 7066
Oldenlandia boscii (DC.) Chapm., SEWP 364; GW 2256; LB 31945
Oldenlandia uniflora L., SEWPLB 486; LB 32810, 32999
**Richardia scabra* L., SEWP 394; MM 7682, SW 107
**Sherardia arvensis* L., WP 114
Stenaria nigricans (Lam.) Terrell, SEWP 233

Saururaceae
Saururus cernuus L., MM 7132

Scrophulariaceae
Bacopa monnieri (L.) Pennell, SEWP 243; MM 7681; SW 112
Gratiola pilosa Michx., LB 32021
Gratiola virginiana L., LB 31938
**Lindernia crustacea* (L.) F. Muell., LB 33014
Lindernia dubia (L.) Penn., LB 32788
Mecardonia acuminata (Walter) Small, SW 76; MM 7223; PM 01; LB 32788
Micranthemum umbrosum (J.G. Gmel.) Blake, SEWP 352; MM 7667
Mimulus alatus Aiton, LB 32787
Nuttallanthus texana (Scheele) Sutton, LB 31944; LBRH 32062
Scoparia dulcis L., MM 7221; SW 79; GW 3360a, 2254
**Veronica arvensis* L., LB 31940

Smilacaceae
Smilax bona-nox L., SEWP 268
Smilax glauca Walter, MM 7145
Smilax laurifolia L., SEWP 417; SW 24
Smilax pumila Walter, MM 7115, 7070
Smilax rotundifolia L., SEWP 274
Smilax smallii Morong, MM 7086

Solanaceae
Solanum carolinense L., MM 7173; LBRH 32068

Symplocaceae
Symplocos tinctoria (L.) L. Her., MM 7116, 7113

Styraceae
Halesia diptera Ellis, SEWPLB 505
Styrax americanus Lam., SW 04

Thelypteridaceae
Thelypteris kunthii (Desv.) C.V. Morton, LB 32480

Ulmaceae
Celtis laevigata Willd., GW 2335
Ulmus alata Michx., SW 56; GW 2334
Ulmus americana L., SEWPLB 493

Urticaceae
Boehmeria cylindrica (L.) Sw., MM 7208; SW 37; LB 3021

Valerianaceae
Valerianella radiata (L.) Dufr., WP 115

Valerianella radiata (L.) Dufr. f. *parviflora* (Dyal) Egg. Ware, LBRH 32053

Verbenaceae
Callicarpa americana L., MM 7084
**Glandularia pulchella* (Sweet) Troncoso, SEWP 256
Phyla nodiflora (L.) Greene, SW 94
**Verbena brasiliensis* Vell., SEWP 258
Verbena halei Small, MM 7143
**Verbena rigida* Spreng., SEWP 257

Violaceae
Viola lanceolata L., MM 7092; LB 33013
Viola palmata L., MM 7159; GW 2295; PM 05
Viola primulifolia L., SW 11
Viola sagittata Aiton, GW 2292
Viola sororia Willd., GW 2294; LB 31986

Vitaceae
Ampelopsis arborea (L.) Koehne, SW 29
Parthenocissus quinquefolia (L.) Planch., SEWP 250
Vitis aestivalis Michx., MM 7079; GW 2428
Vitis rotundifolia Michx., MM 7055

Xyridaceae
Xyris difformis Chapm. var. *difformis*, LBSEWP 31893, 31898; MM 7204, 7237
+*Xyris jupicai* L.C. Rich., SEWP 419, 354, 328; LB 32462

Addendum

Isotria verticillata (whorled pogonia) and sugar maple (probably either *Acer barbatum* or *Acer leucoderme*) are listed for the unit on the Beechwoods Trail Guide, a mimeographed guide available at the trail entrance, but we failed to collect them during our two- year field survey, and could not find herbarium material of same. Geraldine Watson (2006) also indicated that sugar maple (*Acer barbatum*) is making a remarkable recovery in this unit with the removal of cattle grazing.

Notes

Carex section ovales. The specimen in this collection was too immature for specific identification. The only other *Carex* in section *ovales* was *C. brevior.* Perhaps this was an immature *C. brevior.*

Bartonia texana. Currently Beech Creek is the only Big Thicket unit to have this rare Texas endemic. We made two collections, one in a sphagnum mat along the Beechwoods Trail, and one far from any trail, near the intersection of Beech Creek with Little Beech Creek.

Bradburia pilosa. We are following Semple (2006). An equally correct name is *Chrysopsis pilosa* Nutt.

Rhynchospora debilis. This is the third collection for Texas and the first for the Pineywoods. See Brown et al. (2007) for additional information.

Xyris jupicai. There is no consensus as to the native or introduced status of this yellow-eyed-grass.

Discussion

There are 103 families and 229 genera represented for the 470 taxa (418 native) on the Beech Creek Unit list. Eight families: Poaceae (59 taxa), Asteraceae (53 taxa), Cyperaceae (40 taxa), Fabaceae (26 taxa), Lamiaceae (15 taxa), Euphorbiaceae (13 taxa), Scrophulariaceae (11 taxa), and Juncaceae (11 taxa) account for 48.9% of the taxa collected. The largest genera are: *Carex* (15 taxa), *Dichanthelium* (13 taxa), *Rhynchospora* (11 taxa), *Juncus* (10 taxa), *Quercus* (9 taxa), and *Cyperus* (7 taxa).

While it is the case that our list is incomplete, as are all floras, and that a few taxa reported here may no longer exist on the unit, specimens of most taxa that have grown in the Beech Creek Unit during the past quarter century have been collected (probably 95+ %). We estimate that the Beech Creek Unit has about 425 to 450 native species/taxa.

Acknowledgments

This study was supported in part by a National Park Service Cooperative Agreement No. CA 14001004 to Paul Harcombe and in part by an All Taxa Biological Inventory (ATBI) grant to the first author from the Big Thicket Association of Saratoga, Texas. The page charges were paid for from this grant. The first author appreciates Deanna Boensch and Lily Zhou, Big Thicket fire ecologists, for facilitating his passage across private land to the northeast corner of the unit and then walking with him along Little Beech Creek south

to near the confluence with Beech Creek. Eleven new additions to the species list were collected on this all-day hike. Thanks also to Ray C. Telfair II and Eric Keith for many helpful suggestions derived from their careful reading of the paper.

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EARLY HISTORICAL REFERENCES TO THE BIG THICKET, TEXAS

Michael H. MacRoberts and Barbara R. MacRoberts

Bog Research, 740 Columbia
Shreveport, Louisiana 71104, U.S.A.
and Herbarium, Museum of life Sciences
Louisiana State University in Shreveport
Shreveport, Louisiana 71115, U.S.A.

ABSTRACT

We report on four pre-1860 references to the Big Thicket. All place the Big Thicket on or near the San Jacinto River west or at the western edge of where modern accounts place it. Two describe it as a thicket, and two as open woods.

RESUMEN

Citamos cuatro referencias anteriores a 1860 del Big Thicket. Todas colocan el Big Thicket en o cerca de San Jacinto River al oeste o en la orilla oeste de donde lo colocan los modernos. Dos lo describen como un matorral, y otros dos como bosques abiertos.

There is much disagreement on what should be called the Big Thicket (Cozine 2004; Diggs et al. 2006). The broadest conception has it encompassing about 3.5 million hectares in an area extending from the Brazos to the Sabine rivers and from Nacogdoches to Beaumont. The narrowest conception is the "Hunters Thicket" encompassing only 130,000 hectares mostly in Hardin County. Today, the most generally accepted view corresponds more or less to a compromise between the Biological Survey definition of Parks and Cory (1938) and the Ecological Area definition of McLeod (1971). In this view it encompasses more or less Jasper, Newton, Tyler, Hardin, Polk, San Jacinto, Montgomery, and northern Liberty counties: about 1.8 million hectares (see Diggs et al. [2006] for a detailed discussion of literature and maps of the various locations of the Big Thicket).

Del Weniger, the eminent ecological historian of Texas, argued that the phrase "Big Thicket" was not old but dated from only the mid-nineteenth century and that today's location of the Big Thicket is not where it originally was (Weniger 1984). The two earliest (pre-1860) accounts he was able to find which used that phrase were by Don E.E. Braman and J. De Cordoba, from 1857 and 1858, respectively. These accounts place the Big Thicket on the San Jacinto River or between the two forks of the San Jacinto River in what are now San Jacinto, Montgomery, and possibly Walker counties, to the west or at the western edge of where modern scholars locate it (county boundaries have changed considerably since the 1850s) (Fig. 1). These two sources do not describe the Big Thicket as an impenetrable forest but as a highly desirable region of mostly large, dense timber with fertile and productive soil that was already extensively settled by the late 1850s.

Diggs et al. (2006) recently described a third pre-1860s account of the Big Thicket. This is in *A Stray Yankee in Texas*, published in 1853 by Philip Paxton (Paxton 1853). As Diggs et al. (2006) only briefly mention this reference, additional comment seems warranted. Philip Paxton (a pseudonym for Samuel Adams Hammett, 1816-1865) was born in Connecticut and moved to Texas in 1835 where he remained until 1848 working in and around Montgomery and Houston. Upon his return east, he wrote serious and humorous magazine articles about Texas. In 1853 he published these as *A Stray Yankee in Texas* (Hoole 2007). Paxton's account of the Big Thicket is interesting for two main reasons. First, he places the Big Thicket on the San Jacinto River, which, as in the accounts of Braman and De Cordoba, is west of or on the western edge of where current descriptions locate it. Second, unlike Braman and De Cordoba, Paxton describes the Big Thicket as a thicket. According to him, the Big Thicket, while having "the finest timber in the world" is "a thicket so dense that even in that country of tangled forest, it is known—*par excellence*—as the big thicket...." He continues: "This spot had been aptly named the 'big thicket.' Immense bamboo briers, like vegetable *Pythons*,

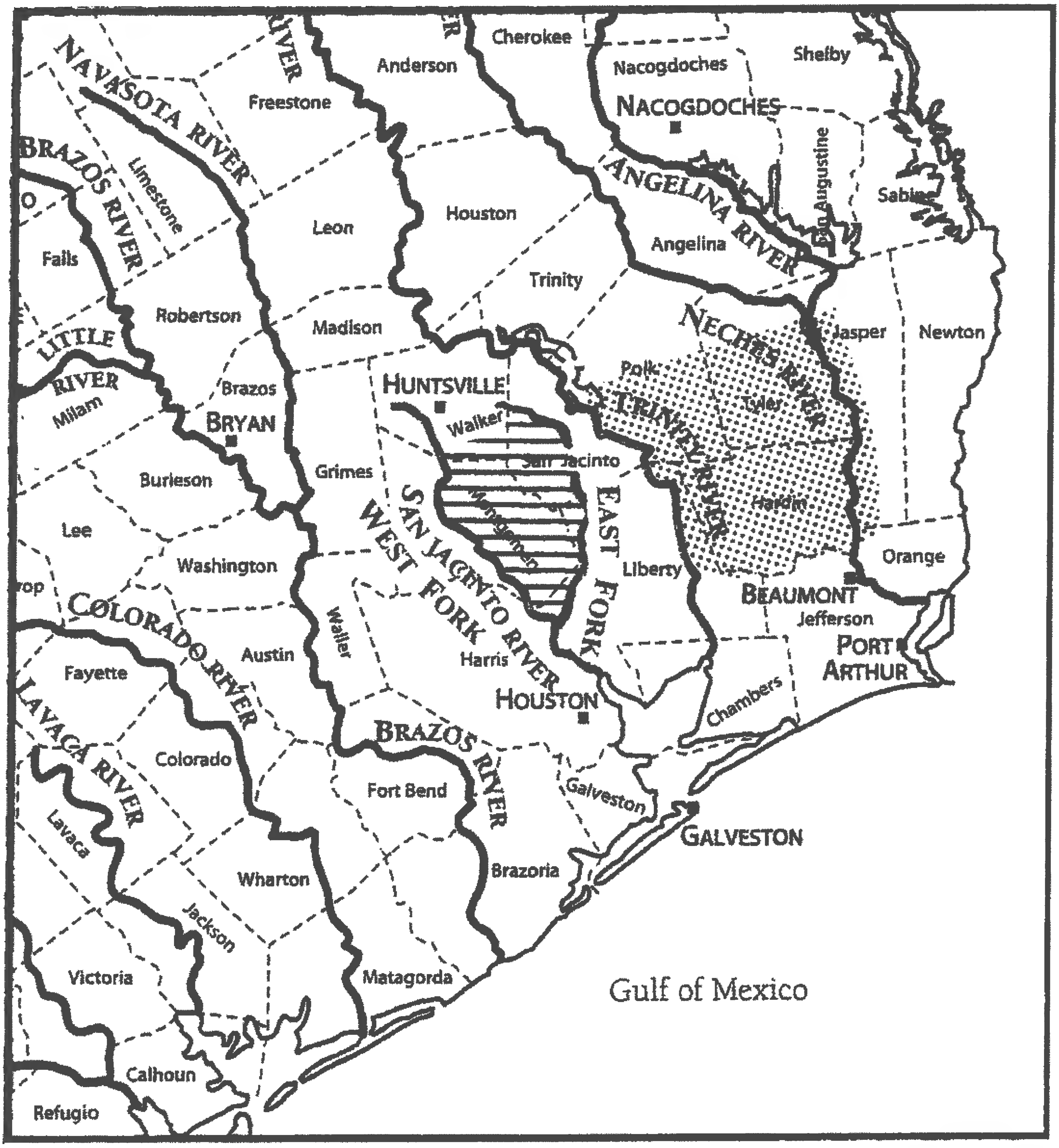

Fig. 1. Southeast Texas showing pre-1860 location of the Big Thicket (hatched area) and present day location of the Big Thicket National Preserve (speckled area) (Figure modified from Diggs et al. 2006, Figure 8).

twined and intertwined, crossed and recrossed, from tree to tree, and shrub to shrub, forming a natural trellis-work for the thousand and one wild and beautiful vines that abound there." Further, he writes: "The first part of our journey was effected on horseback; but after proceeding some half a mile into the 'timber,' this mode of progression was suddenly brought to a period by the dense undergrowth, and we were reduced to a very natural and primitive style of locomotion." Finally, he adds: "We now had to contend for every step we gained; knife and hatchet were in constant requisition, and for one hour we pressed on in Indian file as fast as we could." Paxton describes or refers to such plant habitats as "cypress-brakes," "palmetto swamps," "cane-brakes," "sloughs," and "prairies." He mentions individual plants: "magnolia grandiflora," "bamboo,"

"passion vine," "cypress vine," "morning-glory," "trumpet-creeper," "cypress," "hanging-moss" (Spanish moss), and "cane," and animals: "log-cock" (Pileated woodpecker), "paroquet" (Carolina parakeet), "mocking-bird," "moccasin snake," "alligator," "bear," and "fish."

With the aid of Parker's bibliography (1977), we located another early account. This occurs in an article "The Big Thicket Ruins" in *The Texas Republic*, 3 May 1856. The relevant passage reads: "A man by the name of *Smith*, reported to the Washington American about the *First of April*, that he had recently discovered in the Big Thicket on the San Jacinto some twenty-five miles from Montgomery, an ancient ruin...." (italics in original). The article goes on to describe these ruins as being in "a dense thicket almost impenetrable."

Thus, all four of the earliest known references to the Big Thicket place it on the San Jacinto River or between the forks of the San Jacinto River on the western edge of the generally accepted conception of the Big Thicket (Diggs et al. 2006), or as Weniger (1984) stated: "this places the Big Thicket in the area of present Montgomery and San Jacinto counties, roughly between Conroe, Cleveland, Coldspring, and Huntsville," which is basically what is today the Sam Houston National Forest. To our knowledge, there are no early accounts that place the Big Thicket in Hardin, Tyler, Jasper, Newton, Liberty, or Polk counties or on the Sabine, Neches, or Trinity rivers where present-day scholars locate it and where the Big Thicket National Preserve is located. But, both Paxton's and Smith's accounts contradict Weniger's finding that the Big Thicket was originally described as an open and hospitable land. Both accounts clearly describe the Big Thicket as virtually impassable.

Why and when the phrase "Big Thicket" came to be applied to the more eastern region remains unknown. If anyone knows of other pre-1860 references to the Big Thicket or has information on the evolution of the concept of the "Big Thicket," we would appreciate hearing from them.

ACKNOWLEDGMENTS

We appreciate the reviews by Guy Nesom and George Diggs.

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BOOK NOTICE

Wayne A. Sinclair and Howard H. Lyon. 2005. **Diseases of Tress and Shrubs, Second Edition.** (ISBN 978-0-8014-4371-8, hbk.). Cornell University Press, Sage House, 512 East State Street, Ithaca, New York 14850, U.S.A. (**Orders:** www.cornellpress.cornell.edu, 1-607-277-2211, 1-800-688-2877 fax). $89.95, 660 pp., color plates, companion CD-ROM, 9 1/4" x 12 3/8".

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THE BIG THICKET OF TEXAS AS FLORISTICALLY UNIQUE HABITAT

Michael H. MacRoberts and Barbara R. MacRoberts

Bog Research, 740 Columbia
Shreveport, Louisiana 71104, U.S.A.
and Herbarium, Museum of Life Sciences
Louisiana State University in Shreveport
Shreveport, Louisiana 71115, U.S.A.

ABSTRACT

The Big Thicket is floristically closely related to the southeastern United States. Using species that are unique to the Big Thicket region in Texas, we find here that most are wetland adapted. The Big Thicket is the wettest area of Texas and is edaphically, geologically, physiographically, and climatically continuous with the southeastern United States. Many eastern species appear to reach their distributional limit in southeastern Texas because of the high precipitation and wet condition that characterize this area.

RESUMEN

El Gran Matorral está muy relacionado florísticamente con el sureste de los Estados Unidos. Usando especies que son únicas en la región del Gran Matorral en Texas, hemos encontrado que la mayoría están adaptadas a la humedad. El Gran Matorral es el área más occidental de Texas y tiene continuidad edáfica, geológica, fisiográfica, y climática con el sureste de Los Estados Unidos. Muchas especies orientales tienen su límite de distribución en el sureste de Texas debido a la alta precipitación y condiciones de humedad que caracterizan esta área.

INTRODUCTION

The Big Thicket has been described as an area where many floras converge (see MacRoberts & MacRoberts 2004, 2007; Diggs et al. 2006 for discussion and literature). This characterization has been questioned (MacRoberts & MacRoberts 2004a; MacRoberts et al. 2007). The affinity of the Big Thicket flora is almost entirely within the eastern and especially southeastern U.S.A. (Diggs 2002; Diggs et al. 2006; MacRoberts & MacRoberts 2003, 2004a, 2007; McLaughlin 2007).

The present study originates from a statement in Diggs et al. (2006:171): "While clearly part of the southeastern U.S., the Big Thicket represents the southwestern extreme of the Southeastern Mixed Forest Province and the Outer Coastal Plain Mixed Forest Province.... Hundreds of species that occur in an arc from Virginia or North Carolina south to Florida and west to Texas reach the southern or southwestern limit of their ranges in the Big Thicket, or are confined or largely confined in Texas to the Big Thicket area. The reasons for their occurrence in the Big Thicket include the high rainfall and overall mesic conditions and the presence of specialized habitats...."

As part of a continuing effort to describe and understand the flora of the Big Thicket region (Parks & Cory 1936; Watson 1975; Ajilvsgi 1979; Marks & Harcombe 1981; Bridges & Orzell 1989; Harcombe et al. 1993; MacRoberts & MacRoberts 2004a; MacRoberts et al. 2002, 2007; Brown et al. 2005, 2006a, 2006b, in press; Diggs et al. 2006), we concentrate in this study on what is unique floristically to the Big Thicket region in Texas and how this flora relates to abiotic conditions.

THE BIG THICKET REGION

Southeastern Texas (in which the Big Thicket occurs) is edaphically, geologically, and physiographically related to and continuous with the remainder of eastern Texas and western Louisiana (Fenneman 1938; Godfrey et al. 1973; Groat 1984; Deshotels 1976, Aronow 1981; Bureau of Economic Geology 1992; Shelby et al. 1992; and Diggs et al 2006). What is unique to the Big Thicket region within Texas is its humid subtropical climate (Bomar 1995). Southeastern Texas receives more rainfall than any other area of Texas, northwestern Louisiana, or southwestern Arkansas (Fig. 1) (Owen & Schmidly 1986; Bomar 1995; Goins & Caldwell 1995; Diggs et al. 2006). Rainfall ranges from 122 to 152 cm, making southeastern Texas the westernmost area

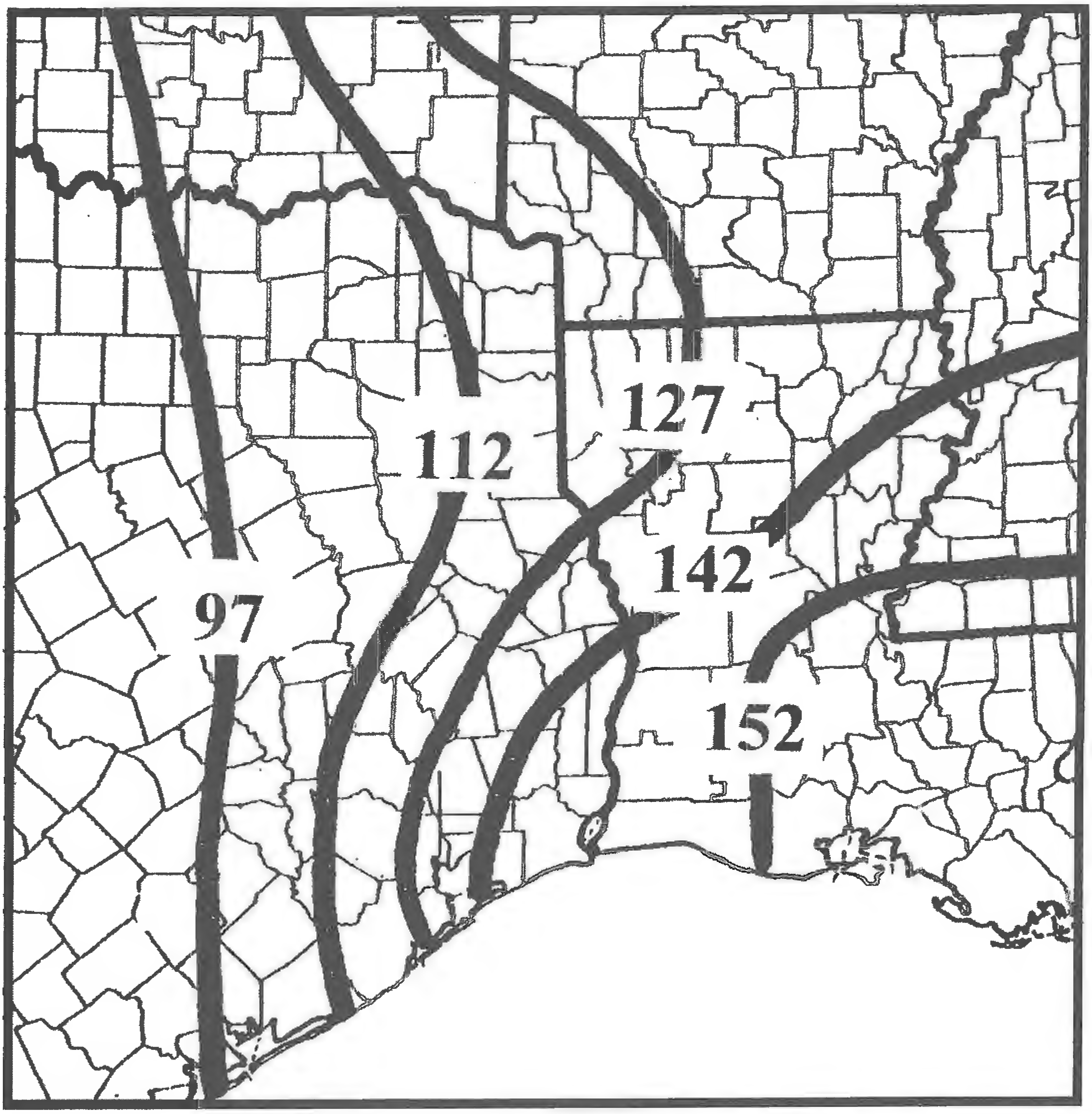

Fig. 1. Annual precipitation (in cm) of the southcentral United States.

of the eastern United States to receive such large amounts of precipitation (Diggs et al. 2006). Additionally, precipitation is well distributed through the year, the difference between driest and wettest month being only a few centimeters (Bomar 1995; Diggs et al. 2006). The only significant variation in elevation in the Big Thicket region is connected to the Willis and Fleming formations to the north where elevation rises to 110 meters and where water runoff is fairly rapid. To the south on the Lissie and Beaumont formations there is little or no relief and the area is poorly drained. Because of high precipitation and flat terrain, soils are often waterlogged, and water may stand for long periods of time in some areas, e.g., wetland pine savannas, baldcypress sloughs, and palmetto-hardwood flats (Bridges & Orzell 1989; Marks & Harcombe 1981; Harcombe et al. 1993; Diggs et al. 2006). Additionally, because of high rainfall, the soils—Ultisols and Alfisols—are often deeply weathered. The relatively low latitude (approximately 30 degrees N) and proximity to the Gulf of Mexico result in uniformly high temperatures and a long humid growing season (Bomar 1995). South-

eastern Texas has the highest net above-ground primary productivity in Texas (Owen & Schmidly 1986), a net primary productivity comparable to the southeastern United States.

METHODS

Using the plant distribution maps in Turner et al. (2003) and Diggs et al. (2006), we developed a list of 98 native species "unique" to the Big Thicket region in Texas. This list consists of all species that are either confined entirely to the Big Thicket in Texas (wherever else they occur in North America) (e.g., *Spiranthes longilabris* Lindl.) or that are concentrated in but not totally confined to the Big Thicket in Texas (wherever else they occur in North America) (e.g., *Xyris scabrifolia* Harper). Using sources available (e.g., Diggs et al. 2006; MacRoberts et al. 2002), we determined in which habitats (communities) these species occur. Some species occur in more than one community; consequently, we divided their representation between those communities. Using USDA (2007), we determined the wetland status of each species. For those with no wetland rank, we either assigned one based on our personal experience, or, if we did not know the species adequately, put them in the "unknown" category. Using Kartesz and Meacham (2005) and *Flora of North America* (1993–2006), we plotted the North American distribution of the species to determine their relationship to other regions.

In order to put the Big Thicket into a larger context, using Turner et al. (2003) and Diggs et al. (2006) we developed a random selected list of 115 native species confined to eastern Texas but that were evenly distributed over the area, not just the Big Thicket, irrespective of wherever else they occurred in North America. As with the Big Thicket list, we determined, where possible, in which habitats (communities) these species occurred and their wetland status. Using the same sources as for the Big Thicket list, we plotted their North American distribution.

For the purposes of the present study, the Big Thicket is defined as Jasper, Newton, Hardin, Tyler, Polk, San Jacinto, and northern Liberty counties. This definition corresponds closely with the "biological" definition of the Big Thicket and is the same as that used by Diggs et al. (2006). Eastern Texas is defined as the area of Texas east of about 97 degrees longitude.

RESULTS

We found 98 species that are either unique to the Big Thicket or that are concentrated in it within Texas (irrespective of where they occur outside Texas). The community preferences, where they could be determined, are given in Table 1: 65 percent of the species favor wetland communities. The wetland status of these species, where known, is given in Table 2: 67 percent are obligate or facultative wetland species. The North American distribution of these species as a percentage of the total is given in Figure 2: 96 percent occur in Louisiana, 94 percent in Mississippi and Alabama, 91 percent in Georgia and Florida, 85 percent in South Carolina, 81 percent in North Carolina, and 56 percent in Virginia, all of which are coastal states. Percentages drop off precipitously for all other states, regions, and provinces.

The eastern Texas sample had 115 species: 19 percent favored wetland communities (Table 1) and 28 percent were obligate or facultative wetland species (Table 2) (the discrepancy between the two figures is probably due to the high number of unknowns and the high number of plants undesignated by USDA [2007]). The North American distribution of these species is given in Figure 3. The distribution is mainly in the South, but also the East in general.

DISCUSSION

In the past, the Big Thicket has been characterized as an area in which the floras of many regions converge. In a recent study (MacRoberts & MacRoberts 2007), we found that the Big Thicket is almost entirely southeastern with a flora composed of species typical of Louisiana, Mississippi, Alabama, and the East in general; not of species typical of western or central states. The only exceptions to this are prairie species (Brown et al. 2002). However, the Big Thicket is not the only part of the West Gulf Coastal Plain that has prairies.

Table 1. Habitat (community) preferences of Big Thicket and eastern Texas species.

Community/habitat	Big Thicket No.	Big Thicket %	East Texas No.	East Texas %
Bog/Wetland pine savanna	38.5	39	5.5	5
Upland longleaf pine savanna/Mixed woods	13.0	13	29.5	26
Pond/Marsh/Lake margin	13.0	13	9.0	8
Stream course	6.5	7	3.03	
Baygall/Seepage slope	6.0	6	4.0	3
Beech/Wet woods	6.0	6	7.0	6
Mesic Hardwood-Pine forest	6.0	6	30.0	26
Xeric sandylands	1.0	1	9.0	8
Unknown	8.0	8	18.0	15
Total	98.0	100	115	100

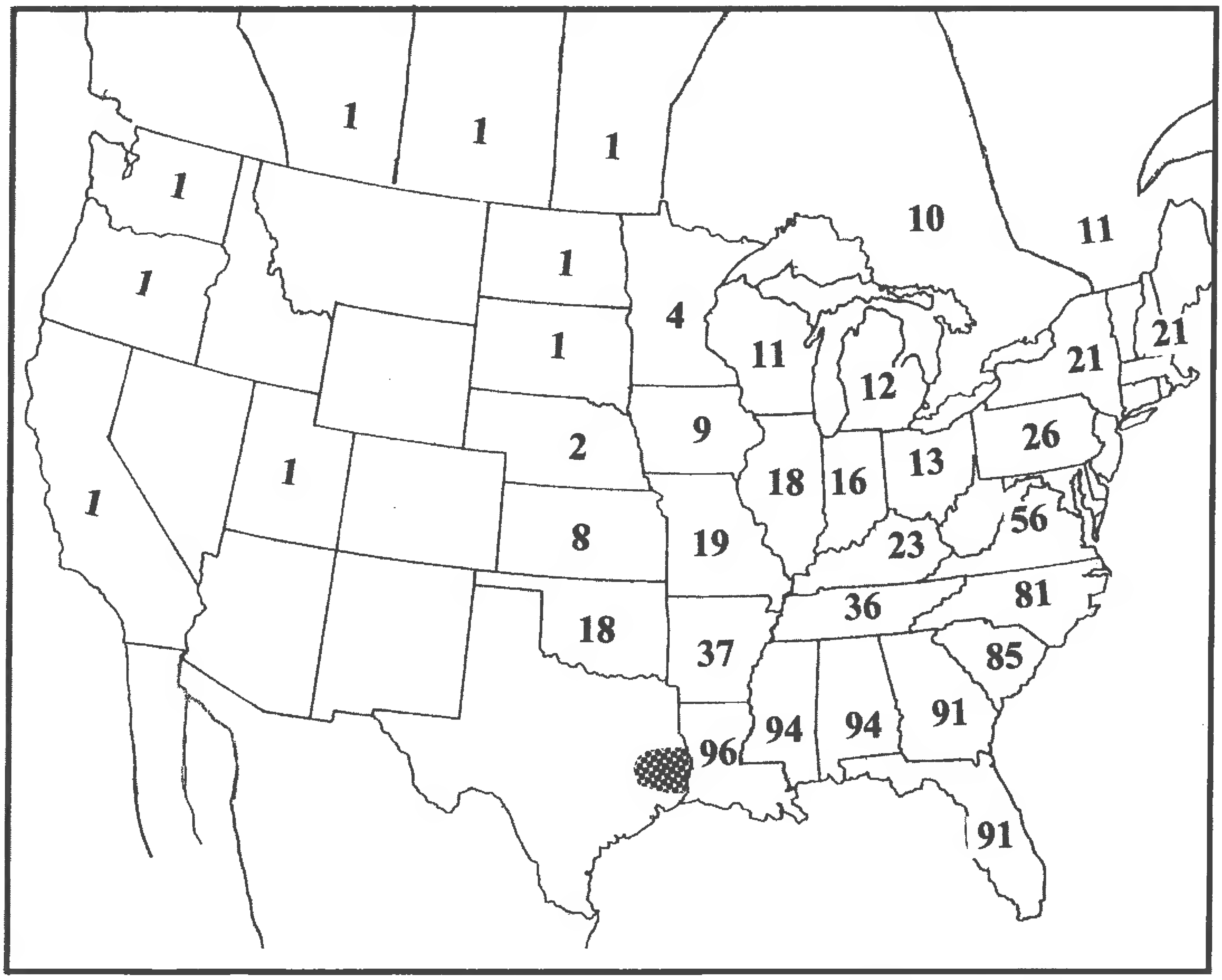

Fig. 2. North American distribution of Big Thicket "unique" species as percentage of total. Stippled area is the Big Thicket.

Prairies are scattered over southeastern Oklahoma, southern Arkansas, western Louisiana, and eastern Texas (MacRoberts et al. 2003; MacRoberts & MacRoberts 2004b).

In the present study, we have extended our earlier analysis of the Big Thicket flora by isolating species unique to the southeastern region in Texas and examining the edaphic, geologic, physiographic, and climatic

Table 2. Wetland status of Big Thicket and eastern Texas species (see USDA [2007] for explanation of status designations).

Status	Big Thicket No.	Big Thicket %	East Texas No.	East Texas %
OBL (obligate wetland)	30	31	13	11
FACW (facultative wetland)	35	36	20	17
FAC (facultative) (intermediate)	14	14	37	32
FACU (facultative upland) (dry)	12	12	30	26
UPL (upland) (very dry)	5	5	13	11
Unknown	2	2	2	2
Total	98	100	115	100

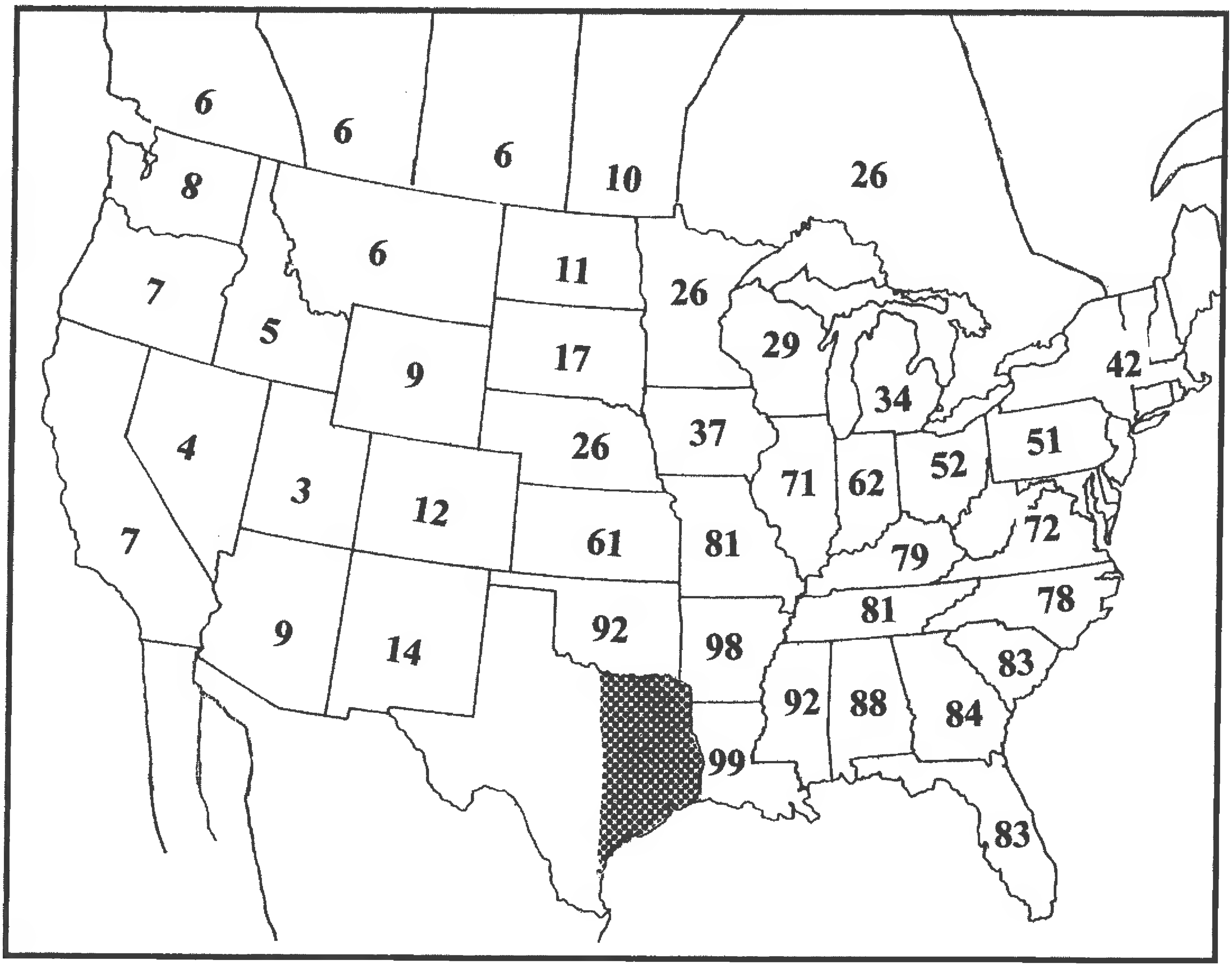

Fig. 3. North American distribution of eastern Texas species as percentage of total. Stippled area is eastern Texas.

uniqueness of the region. As might be expected, considering that southeastern Texas is humid subtropical and the wettest area in Texas, the plants are largely wetland species. Also not unexpected, considering that the southeastern United States has virtually the same climate as does southeastern Texas and that both areas are edaphically, geologically, and physiographically similar, plants that are unique to the Big Thicket in Texas are also found in Louisiana, Mississippi, Alabama, Florida, Georgia, Virginia, and the Carolinas, all of which are coastal states with high rainfall and thus deeply weathered soils.

This conclusion is supported by our analysis of the eastern Texas plant group. While two-thirds of

the species confined to the Big Thicket region are wetland species, only one-quarter of the eastern Texas group are. Additionally, the North American distribution of these species is significantly different from the Big Thicket group. Instead of hugging the southern coastal states, they are distributed across eastern North America.

Further support for the thesis that the Big Thicket is characterized floristically by wetland plants is offered by Diggs et al. (2006:169), who found that the Big Thicket is relatively rich in monocots when compared to other areas of Texas. They speculate that this difference probably relates to high percentage of mesic to wet habitats favored by many monocot species.

Another indicator of the importance of precipitation in the Big Thicket is the presence of drought-intolerant American beech (*Fagus grandifolia* Ehrh.), which reaches its westernmost limit in the United States in Montgomery and San Jacinto counties (McLeod 1975; Diggs et al. 2006).

In conclusion, southeastern Texas and thus the Big Thicket is the westward abiotic extension of the southeastern United States and thus also its westward phytogeographic extension. Many southeastern species reach their distributional limit in southeastern Texas because of its high precipitation and edaphic conditions resulting from that high precipitation.

Thus, as Diggs et al. (2006) point out, the Big Thicket represents a biological boundary and is therefore important for a number of reasons. For example, populations at the margin of a species' range are often unique genetically and represent an irreplaceable resource. Also, peripheral populations are often more sensitive to environmental change and can act as ecological indicators. More locally, the Big Thicket is important because it is a unique area within Texas, and the Big Thicket National Preserve is one of the few relatively large protected areas in the entire West Gulf Coastal Plain serving as a refuge not only for species and communities in Texas but the entire area as well.

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BOOK NOTICE

Richard H. Waring and Steven W. Running. 2007. **Forest Ecosystems: Analysis at Multiple Scales, Third Edition.** (ISBN 978-0-12-370605-8, pbk.). Elsevier Academic Press, 30 Corporate Drive, Suite 400, Burlington, Massachusetts 01803, U.S.A. (**Orders:** www.books.elsevier.com, 1-800-545-2522, 1-800-568-5136 fax, Elsevier, Order Fulfillment, 11830 Westline Industrial Drive, St. Louis, Missouri 63146, U.S.A.). $69.95, 420 pp., maps, figures, tables, some color plates, 7 1/2" × 9 1/4".

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SEED GERMINATION RESPONSE OF *ZIZANIA TEXANA* (POACEAE: ORYZAE) TO SOIL INUNDATION

M.L. Alexander

U.S. Fish and Wildlife Service
San Marcos National Fish Hatchery and Technology Center
500 E. McCarty Lane
San Marcos, Texas 78666, U.S.A.

ABSTRACT

Although the current distribution of *Zizania texana* (Texas wild rice) supports the theory that this species requires flowing water for stable existence, historical documents describe the plant as growing bank to bank within the San Marcos River, Hays County, TX, U.S.A. This may mean that, at times, *Z. texana* grew without flowing water or germinated in saturated, but not inundated soils. In this study, I determine if *Z. texana* requires water-inundated soil for successful seed germination. I found that although some seeds will germinate without inundated soils, the germination success of the groups of seeds tested in inundated soils was significantly higher ($p< 0.01$) than those tested in only saturated soils. The results of this study may help with future restoration and recovery of this endangered species.

RESUMEN

A pesar de que la distribución actual de *Zizania texana* (arroz tejano silvestre) en peligro de extinción respalda la teoría de que esta especie requiere agua corriente para su existencia estable, documentos históricos describen esta planta creciendo de ribera a ribera en el Río San Marcos en Hays County, TX, USA. Es posible que esto indique que, en algunas ocasiones, *Z. texana* creció sin agua en circulación, o germinó en tierras saturadas pero no inundadas. En este estudio, se determinó si *Z. texana* requiere tierra inundada para el éxito en su germinación. Encontré que a pesar de que algunas semillas germinan sin tierras inundadas, el éxito de germinación de grupos de semillas puestas a prueba en tierras inundadas fue significativamente más alta ($p< 0.01$) que aquellas probadas en tierras saturadas. Los resultados de este estudio puede que ayude en los esfuerzos futuros de restauración y recuperación de esta especie en peligro de extinción.

INTRODUCTION

Ecophysiology of seed germination is very important for the conservation of endangered species as it is a key factor of reproduction and will therefore strongly aid in restoration strategies. For aquatic and wetland plants, it is essential to know if germination rates are affected by soil water-levels (Sifton 1959; van der Valk 1981; Keddy & Ellis 1985; Kellogg et al. 2003). This information will help in making decisions regarding where in an aquatic system seeds should be planted.

There are three species in the genus *Zizania* L. in North America: *Z. aquatica* L., *Z. palustris* L., and *Z. texana* Hitch (Terrell et al. 1997). Each of these species grow in aquatic environments, but *Z. texana* may require flowing water for stable existence (Power 1996; Poole & Bowles 1999), while the other species can be found in stagnant water on the edges of lakes or along muddy shores of slow-moving streams that are subject to constant changes in water levels (Archibold & Weichel 1986; Pip & Stepaniuk 1988). *Zizania texana* is a federally listed endangered species endemic to the San Marcos River, San Marcos, Hays County, Texas, U.S.A. The distribution of *Z. texana* is restricted to the upper 2.4 km of the river, within mean water depths ranging between 0.72 to 0.83 m, and mean velocities ranging between 0.38 to 0.93 m/s (Poole & Bowles 1999).

Historical documents that portray *Z. texana* growth in the San Marcos River describe the plant as growing bank to bank, including irrigation waterways (Silveus 1933; Terrell et al. 1978). The San Marcos River is spring-fed and river flow relies on the spring outflow as well as runoff. When outflow and runoff are low, such as during times of drought, the area near the banks may not always be covered by water. This may mean that, at times, *Z. texana* grew without flowing water or germinated in non-inundated soils. The purpose of this study was to evaluate the response of seed germination of *Z. texana* to soil inundation. For this study, I test the hypothesis that *Z. texana* seeds need to be in inundated soil for successful germination.

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MATERIALS AND METHODS

Approximately 3,375 cm^3 of soil consisting of one third pea gravel to two thirds of an equal mixture of compost, top soil and sand was placed into each of 10, 45 x 30 x 13 cm clear plastic rectangular containers. Soil mixtures were saturated with water from the Edwards aquifer (the same water source as the San Marcos River) until the point at which pooled water just began to become visible on top of the soil. Seeds used for the study were collected randomly from container grown plants growing in the San Marcos National Fish Hatchery and Technology Center that were initially collected from the San Marcos River following techniques recommended by Richards et al. (2007) for the best genetic representation of the wild population. We used a total of 50 seeds for this study. Because this endangered plant has such a small population size, there are only a small number of seeds available for scientific studies. The seeds were collected four months prior to the experiment, in September 2006, and preserved in a refrigerator at 4 °C in moist paper towels within sealed plastic bags, allowing for optimal germination conditions (Rose & Power 2001). Lemna and palea were kept intact as their presence does not change germination probability and as it also mimics the natural condition in this species (personal observation). Five seeds of approximately equal size were placed equidistant to each other (5 cm apart) in the containers of saturated soil at a ¼ cm depth. All containers were placed into a growth chamber set to a 12-hour photo period at 20 – 23 °C. Water was added slowly to the five containers receiving the inundated treatment until it covered the soil with 2.5 cm of water. Each inundated treatment was paired next to a non-inundated treatment within the growth chamber. Every 24 hours, any water loss within the 10 containers was compensated for, seeds were visually examined for signs of germination, and the total number of germinated seeds was recorded. Seeds were considered to have germinated when the radical had visibly emerged from the pericarp. Since Power and Fonteyn (1995) found that most seeds of *Zizania texana* germinate within a 10-day period, following a 4-week period of daily visual examinations the study was terminated. A paired t-test was run in order to determine if there is a significant difference between the germination success rates of the two treatments, non-inundated and inundated (analysis performed using SYSTAT v.10 statistical package).

RESULTS

Sixteen of the 25 total seeds in inundated soil and four of the 25 total seeds in non-inundated soil germinated within the 4-week period (Fig. 1). Germination success was greater in inundated soil than in non-inundated soil (paired $t = 4.7$, $df = 8$, $p = 0.009$; Mean difference = 2.4; 95% C.I. = 0.98 to 3.82).

DISCUSSION

In this study, more *Z. texana* seeds germinated in inundated soil than in non-inundated soil. This may be because *Z. texana* seeds are recalcitrant and do not survive for long outside of water (Horne & Kahn 2000). The seeds may more readily germinate in inundated soil than in non-inundated soil because *Z. texana* are so sensitive to desiccation.

Zizania texana is considered a perennial grass (Terrell 2007). In its current distribution within the San Marcos River, *Z. texana* plants are, for the most part, submerged year round (personal observation) and rarely flower (Emery 1966, 1977). There is a possibility that the species has an annual form as well in certain environments. This species is a CO_2 obligate (Power & Doyle 2004). It may remain in perennial form if growing in current velocities such that the boundary layer surrounding the leaves is small enough to take in CO_2 for photosynthesis. However, if in stagnant, or slow moving currents, an individual plant may become emergent in order to take in CO_2 from the air (where it is much more abundant), flower, seed, and then die (i.e., annual growth form). If this species were to grow in its historic range of bank to bank, it may be possible that some of the plants would become annuals and grow in areas of low flow and shallow water. Because the seeds do not germinate as well in non-inundated soil, the San Marcos spring-flow has to continue to be high enough (>100 cubic feet per second) that the soil at the banks' edge is consistently inundated. Currently, *Z. texana* is inhibited from growing along the shallow, low flow banks because *Colo-*

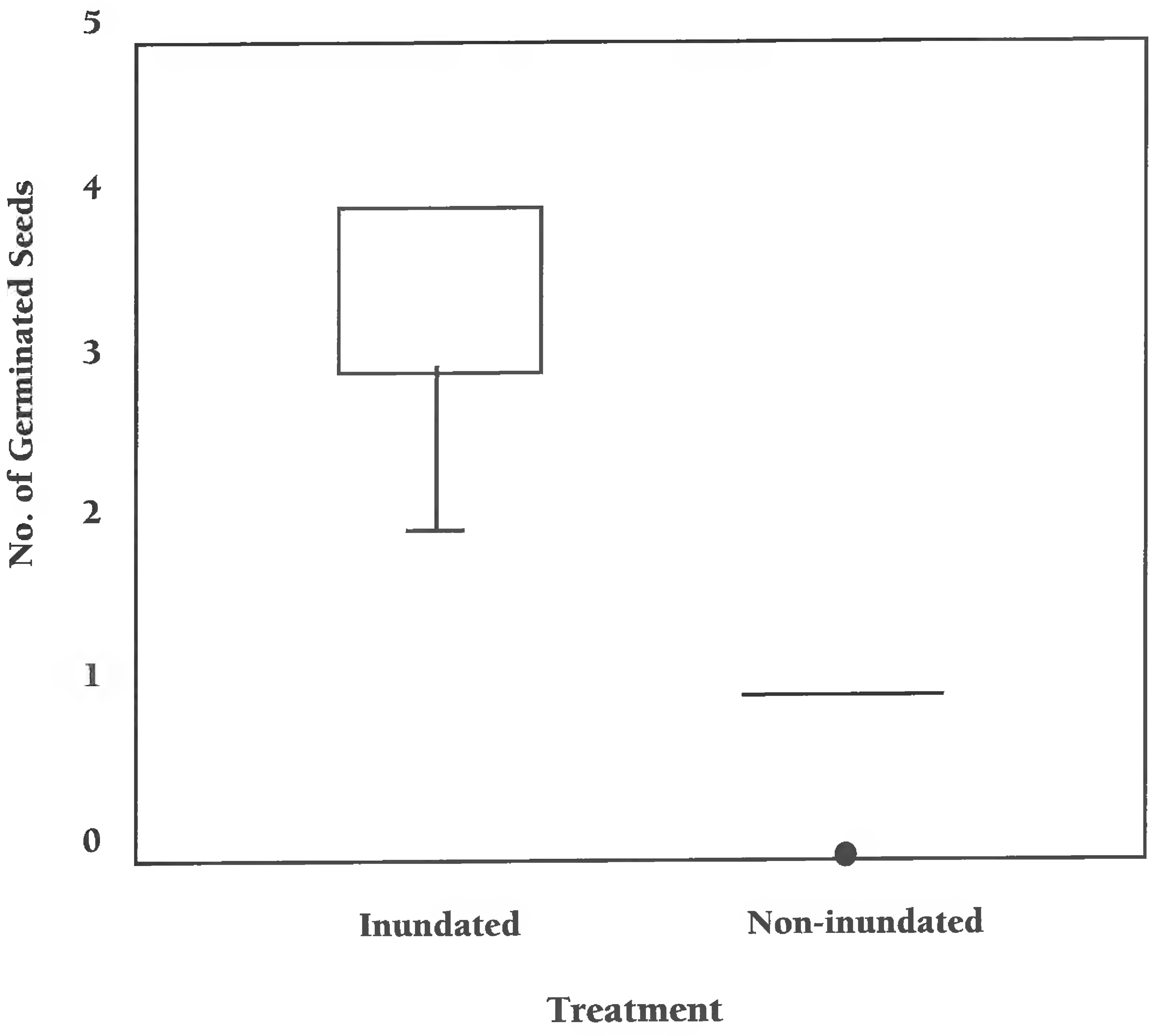

Fig. 1. A box plot portraying the median number of germinated *Zizania texana* seeds in the five containers for each treatment (inundated and non-inundated soil), corresponding quartiles and outliers.

casia esculenta (wild taro) has invaded and dominated the edges of the San Marcos River (Akridge & Fonteyn 1981; Nelson & Getsinger 2000).

The results of this study will aid in future restoration efforts for this endangered aquatic plant. With data that supports the planting of seeds in inundated soil, all areas chosen for planting should be covered in water during average spring flows. Restoration efforts of *Z. texana* should include planting in both low and high flow areas to support both perennial and annual forms of the plant. This would have to include the removal of *C. esculenta* in order to make the river-edge habitat available for the endangered *Z. texana*.

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PREDICTING *VIOLA GUADALUPENSIS* (VIOLACEAE) HABITAT IN THE GUADALUPE MOUNTAINS USING GIS: EVIDENCE OF A NEW ISOLATED POPULATION

Timothy C. Mullet
Department of Biology
Sul Ross State University
Alpine, Texas 79832, U.S.A.

Fred Armstrong[1]
Resource Management Office
Guadalupe Mountains and NP
Salt Flat, TX 79847, U.S.A.

Benjamin Zank
Resource Management and Science
Great Smoky Mountains NP
Gatlinburg, Tennessee 37738, U.S.A.

Christopher M. Ritzi
Department of Biology
Sul Ross State University
Alpine, Texas 79832, U.S.A.

ABSTRACT

Viola guadalupensis is a rare endemic of the Guadalupe Mountains in West Texas. Isolated to a remote limestone, rock face, this species was known only to exist at a single location along the East Rim of Frijole Ridge within Guadalupe Mountains National Park (GMNP). Despite traditional surveys in seemingly suitable habitat, researchers had been unable to locate new populations. Its small population size, genetic isolation, and lack of significant habitat information make this species vulnerable to extinction. Consequently, the Resource Management Office of GMNP has implemented a strategy to introduce laboratory-germinated plants to new sites in an attempt to preserve this species' viability. Geographical Information Systems (GIS) have previously been successful at predicting suitable habitats of rare species; therefore, we developed a GIS-based habitat model – generated from the elevation, aspect, and slope specific to the type locality – that displayed a map predicting suitable *V. guadalupensis* habitat throughout the park. We ground-truthed nine of the 14 locations produced by the habitat model. One location accurately predicted the type locality, while a second location revealed a new population of *V. guadalupensis* within a steep, slot-canyon drainage along Frijole Ridge. Three locations were determined to be suitable for *V. guadalupensis* introduction and four were considered unsuitable. Considering our model accurately predicted the type locality and discovered a new population, despite traditional survey efforts, the usefulness of GIS-based habitat models for surveying rare species is reaffirmed, providing baseline information for further investigation.

Key Words: Geographical Information System, GIS, Violaceae, *Viola guadalupensis*, Guadalupe Mountains, habitat model, validation

RESUMEN

Viola guadalupensis es un endemismo raro de las montañas Guadalupe en el oeste de Texas. Aislada en una pared caliza apartada, esta especie se conocía en una sola localidad a lo largo del borde este del Frijole Ridge en el Guadalupe Mountains National Park (GMNP). A pesar de las tradicionales búsquedas en hábitats aparentemente apropiados, los investigadores no habían localizado nuevas poblaciones. Su pequeño tamaño poblacional, aislamiento genético, y la falta de información sobre el hábitat hizo a esta especie propensa a la extinción. Consecuentemente, la Resource Management Office del GMNP ha implementado una estrategia para introducir plantas germinadas en laboratorio en nuevos lugares en un intento de preservar la viabilidad de esta especie. Los Sistemas de Información Geográfica (GIS) han tenido éxito al predecir hábitats adecuados para especies raras; por ello, desarrollamos un modelo de hábitat basado en GIS—generado a partir de la altitud, aspecto, y pendiente específica de la localidad tipo– que mostró un mapa que predecía los hábitats adecuados para *V. guadalupensis* en todo el parque. Comprobamos sobre el terreno nueve de las 14 localizaciones producidas por el modelo de hábitat. Una localización predijo con precisión la localidad tipo, mientras que una segunda localización reveló una nueva población de *V. guadalupensis* en una grieta de un cañón abrupto de drenaje en la Frijole Ridge. Se determinaron tres localizaciones como adecuadas para la introducción de *V. guadalupensis* y cuatro fueron consideras inadecuadas. Considerando que nuestro modelo predijo con precisión la localidad tipo y descubrió una nueva población, a pesar de los esfuerzos tradicionales de reconocimiento, se reafirma la utilidad de los modelos de hábitat basados en GIS para el estudio de especies raras, aportando un punto de referencia para investigaciones posteriores.

Habitat models developed from Geographical Information Systems (GIS) are useful tools for predicting the distribution of rare species, decreasing the ineffectiveness of random surveys, providing potential sites for relocation, and aiding the overall development of conservation management plans (Vogiatzakis 2003; Imm et al. 2001; Wu & Smeins 2000). Van Manen et al. (2005) developed a predictive GIS-based habitat model

[1]**Correspondent: fred_armstrong@nps.gov**

derived from the variables of known plant locations for a variety of species in Shenandoah National Park, VA. The efficacy of their predictive model at locating species of interest was 4.5 to 12.3 times more efficient than random surveys. Husveth (2003) used a baseline GIS model generated from observed plant locations, surficial geology, and major soil associations to predict likely sites for rare plant species in a 15,378 ha plot of Anoka County, MN. Field validation surveys (i.e. ground-truthing) of this model revealed additional rare plant populations as well as high to medium quality habitats for rare species. Although the predictive capabilities of GIS-based models are only as good as the variables used to generate them, they can provide useful insight into the dependency of rare species on habitat variables.

The Guadalupe Mountains violet (*Viola guadalupensis* Powell & Wauer) is a rare and unique species of wildflower endemic to the highest elevations of the Guadalupe Mountain range in West Texas. The species was described in 1990 within Guadalupe Mountains National Park (GMNP; Fig 1), Culberson County, TX, and since its discovery has only been recorded from a single location along the East Rim of Frijole Ridge (Fig 2; Powell & Wauer 1990).

At its type locality, this perennial, yellow-flowered violet grows in mats of up to 20 individuals rooted in small openings of a northwest-facing, dolomitized, limestone rock face approximately 2,600 m above sea level (Powell & Wauer 1990). The plants are well shaded by two large Douglas firs (*Pseudotsuga menziesii* Mirb.) and grow in association with rock spiraea (*Petrophytum caespitosum* [Nutt.] Rydb.), Guadalupe valerian (*Valeriana texana* Steyernm.), small rocklettuce (*Pinaropappus parvus* Blake.), Guadalupe leastdaisy (*Chaetopappa hersheyi* Blake.), littleawn needlegrass (*Achnatherum lobatum* Swall.), and a species of sedge (*Carex sp.*; Powell & Wauer 1990).

Little is known about this species' natural history or the specific habitat characteristics needed to maintain its viability. Speculation has been made of its dependency on microclimatic conditions and substrate type; however, these data have only recently been recorded (F. Armstrong, pers comm.). Average temperature from January 2003 to January 2004, at the type locality, was approximately 12.78°C. Relative humidity during the same time interval ranged from <10 to 100% and daytime light intensity during the growing season (May through July 2002) averaged 0.22 log lum/m^2 (F. Armstrong 2004, unpubl. report). To produce rootstalks for chromosome counts, attempts to germinate seedlings in the laboratory discovered that chilling seeds and treating them with gibberellic acid allowed for successful germination (n = 5; C. Blaxland, pers comm.). Seedlings in potting soil became chlorotic, but when lime was added they regained green coloration indicating an affinity for alkaline substrate (C. Blaxland, pers comm.). Although baseline data have been collected, no intensive comparative analysis or significant research has been done at the risk of damaging the population.

Thorough investigations to locate additional populations in seemingly suitable habitat have been conducted along 8 km of the East Rim of Frijole Ridge from the top of Bear Canyon to Lamar Canyon (Powell & Wauer 1990). Despite these efforts, no other populations were found. *Viola guadalupensis* is currently categorized as a National Park Service Species of Concern, yet it appears to be in danger of extinction based on its small population size and lack of significant habitat information. Powell and Wauer (1990:1) had even commented that *V. guadalupensis* "is an immediate candidate for endangered status" for these very reasons.

With this in mind, the Resource Management Office of GMNP has implemented a plan to collect seeds and germinate them in a laboratory setting with the intentions of introducing *V. guadalupensis* to other suitable locations within the park. The objective of this study was to locate suitable *V. guadalupensis* habitat sites within GMNP, using a GIS-based habitat model generated from variables unique to the type locality, and validate those locations with ground surveys.

METHODS

Study Area.—Our study was conducted within the 34,971 ha of GMNP, Culberson County, TX. The Guadalupe Mountain range is a unique biological sky island consisting of Chihuahuan Desert vegetation (*Agave*,

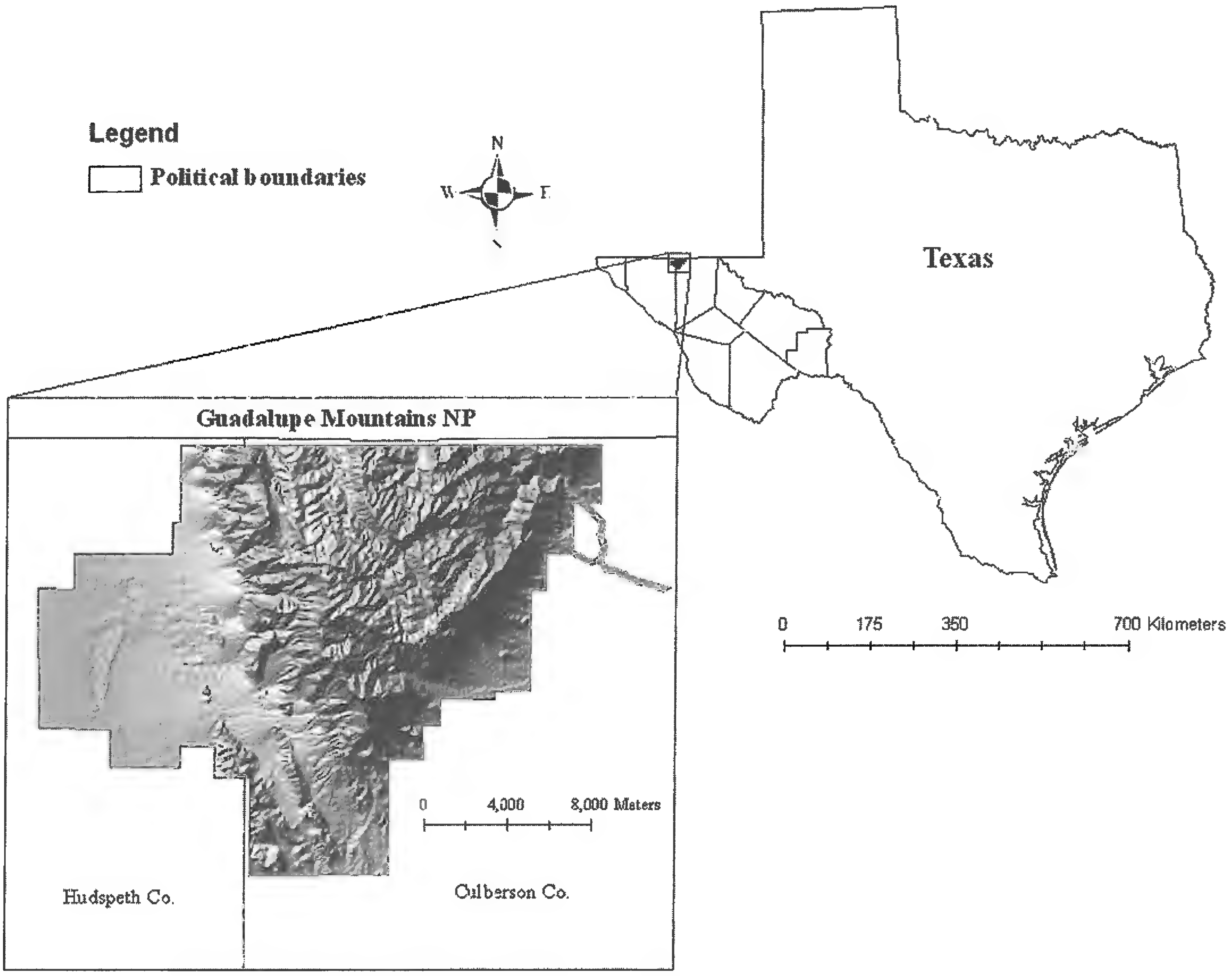

Fig 1. Shaded relief of Guadalupe Mountains National Park located in Culberson and Hudspeth Counties of West Texas.

Yucca, Larrea, Acacia, etc.) at lower elevations (< 2,000 m) and mixed-conifer woodlands of *Pseudotsuga menziesii*, southwestern white pine (*Pinus strobiformis* Engelm.), ponderosa pine (*P. ponderosa* Laws.), pinyon pine (*P. edulis* Engelm.), and various species of oak (*Quercus* sp.) at higher elevations (> 2,000 m). This unique mountain range of the Chihuahuan Desert is the largest limestone uplift in the southwestern United States, formed 250 million years ago by an ancient reef system (Murphy 1984). Mountain summits exceed heights of 2,600 m, shadowing deep canyon systems containing a variety of mountain springs. A 19-year average of temperature and precipitation collected at the 2,455-m elevation automated weather station documented average winter lows of -1.7°C, average summer highs of 23.9°C, and average annual precipitation of 45.0 cm (National Park Service 2005).

Monitoring the type locality.—The condition of the type locality was monitored on 26 May 2006. We compared the counts of individual *V. guadalupensis* plants to a detailed line drawing of individual *V. guadalupensis* plant locations and numbers produced by the Guadalupe Mountains Resource Management Specialist during inventories conducted in 2001, 2002, and 2004. To avoid over estimating the population size, individual plants were conservatively tallied and then averaged between counts for consensus.

GIS model development.—Based on the fact that *V. guadalupensis* had not been observed by park staff or researchers in any of the mesic regions surveyed within the park, we speculated that this species may have specific topographic habitat preferences that include 1) elevations with overall cooler, moister conditions, 2) aspects with minimal hours of direct sunlight, and 3) vertical rock versus horizontal soil substrate as indicated at the type locality. The National Park Service Intermountain Regional GIS Office, in

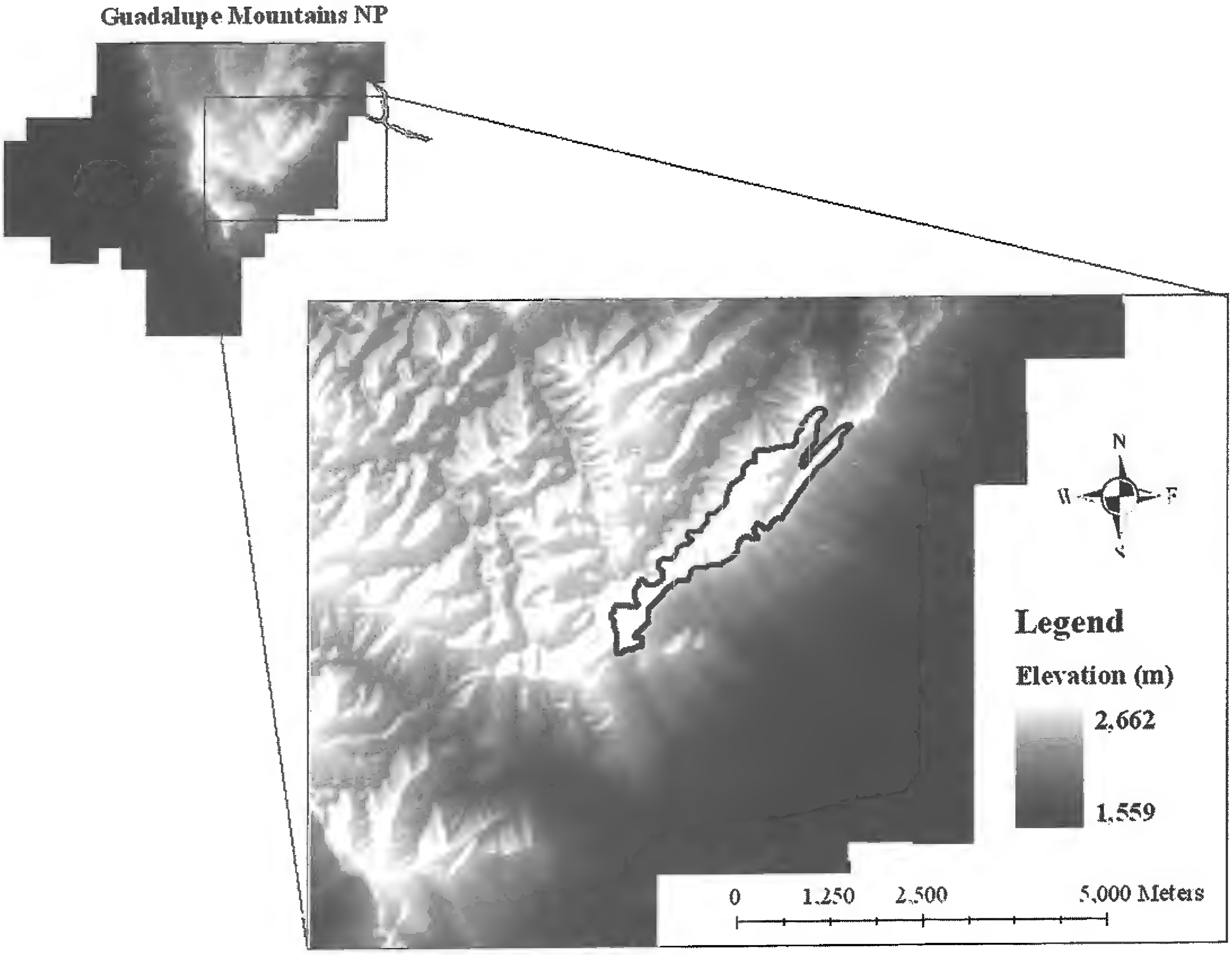

Fig 2. Detailed elevation relief of the East Rim and Frijole Ridge (outlined in black) of Guadalupe Mountains National Park, Culberson Co., TX.

conjunction with GMNP, performed habitat modeling based on these variables to narrow the search areas for potential habitat and suitable locations for establishing additional colonies.

GIS modeling was performed with ESRI's ArcMap Ver. 9.1 software (available from *http://www.esri.com/software/*) incorporating the following parameters in order of priority: 1) elevation bands from 7,800 to 8,000 ft (feet were used for the ease of visually correlating potential sites to USGS topographic maps printed with 40-ft elevation contour intervals), 2) a northwest aspect range from 300 to 330 degrees, and 3) slopes >70 percent. Elevation, aspect, and slope were all derived from a 30-m digital elevation model (DEM) of GMNP obtained from the National Park Service, Natural Resource GIS Data Store.

Using ESRI's ArcToolbox Reclassify tool, DEM cell values were used to separate elevation and aspect into three classes (Class 1 = elevations between 3,500 and 7,800 ft and aspects 0 to 300 degrees, Class 2 = elevations from 7,800 to 8,000 ft and aspects 300 to 330 degrees, and Class 3 = elevations > 8,000 ft and aspects 330 to 360 degrees). The Raster Surface Slope tool was used to divide slope values into two classes (Class 1 = slopes 0 to 70% and Class 2 = slopes >70%). Each class of elevation, aspect, and slope was then assigned a model value of 3, 2, 1, or 0. A model value of three was assigned to the elevation parameters met by Class 3, while model values of 2 and 1 were assigned for the aspect and slope parameters in Class 2, respectively. An assignment of 0 represented all other non-target cell values for every class.

All four model values were unioned together producing a model with seven categories from 0 to 6 displayed as a digital predictive habitat map. Category 0 displayed all non-target parameters; categories 1 and 2 displayed only slope and aspect, respectively. Category 3 displayed criteria for elevation or a combination

of slope and aspect. Category 4 displayed areas where a combination of elevation and slope criteria were met, while Category 5 represented areas of both elevation and aspect. Finally, Category 6 displayed locations where all three parameters of elevation, aspect, and slope were met (Table 1).

Model Validation.—Field validation surveys of predicted *V. guadalupensis* sites were conducted May through July 2006. We used Universal Transverse Mercator (UTM) coordinates digitized in ArcMap to find predicted sites where all three criteria were met (i.e. Category 6). A radius of 200 m was investigated around each UTM location to compensate for any inaccuracies of positioning due to poor satellite geometry. The specific characteristics used to determine suitable habitat of predicted locations in the field consisted of north to northwest-facing rock walls with crevices and vegetation similar to that of the type locality, a physically cooler ambient temperature, and shaded areas with sufficient canopy cover to protect the site from direct sunlight. Rock faces <3 × 3 m were ruled out as insufficient space for colonization due to the lack of potential dispersal of plants within the area.

RESULTS

Status of the type locality.—Compared to previous inventories, 20 new individual plants (n = 94) were recorded in 2006. Although no violets were observed to be flowering, several plants possessed seed capsules. No conspicuous differences in vegetative composition were observed when compared to detailed line drawings and photographs from previous inventories.

Model validation -- The model displayed 14 locations meeting all three criteria in Category 6. We investigated a total of nine locations consisting of three sites near Guadalupe Peak (WGP, NGP1, and NGP2), two near Bush Mountain (BMD1 and BMD2), one north of the Bowl (NOB), one near South McKittrick Canyon (SMK), and two locations on Frijole Ridge. Five locations were omitted from investigation due to inaccessibility and by request of the GMNP Resource Management Office, therefore, no site codes were assigned to these locations.

Two of the nine investigated locations predicted by the model on Frijole Ridge revealed populations of *V. guadalupensis*. One of these locations was the type locality (designated VIGU1). The second location revealed a new, isolated population of *V. guadalupensis* in a steep, slot-canyon drainage (approximately 2.1 to 2.4 m wide), on a 35 degree, northeast-facing limestone wall. The site (designated VIGU2) is located off a plateau on the East Rim approximately 2 km northeast of the type locality.

We observed 25 individual *V. guadalupensis* plants at VIGU2 on 26 May 2006, growing largely in a monoculture. Several *V. guadalupensis* plants were located approximately 1.5 m overhead, making an exact count difficult. Although no seed capsules were observed on non-flowering plants, a number of violets still possessed flowers. All violets had noticeably longer petioles and grew predominantly as individual plants rather than in the mat clusters characteristic of violets at the type locality (VIGU1).

Associated plant species of VIGU2 included *Valeriana texana*, bedstraw (*Galium* sp.), and red alumroot (*Heuchera rubescens* L.). Violets were shaded by the steep, canyon walls and a canopy of western hophornbeam (*Ostrya knowltonii* Cov.) and *P. strobiformis*. Other surrounding vegetation consisted of mountain spirea (*Holodiscus dumosus* Nutt.), *Pseudotsuga menziesii*, and *Petrophytum caespitosum*.

Three of the seven sites without violets (WGP, BMD2, and SMK) were considered to be suitable for introduction upon comparison to the type locality. The remaining four locations (NGP1, NGP2, NOB, and BMD1) were considered unsuitable, possessing sparse vegetation and fully exposed rock faces atypical of either violet location.

Twenty-two percent of all survey sites predicted by the model had extant populations of *V. guadalupensis*. Three of the nine sites (33%) were considered to be suitable sites for introduction. Overall, this model had 56% accuracy for predicting suitable or existing *V. guadalupensis* habitat.

Potential locations for introduction.—The first site considered to be suitable was located around WGP and appeared to be very similar to that of VIGU1. This site (designated WGP1) included a steep rock face, shaded by several small *Pseudotsuga menziesii* and *Ostrya knowltonii* trees approximately 40 m down a

Table 1. Assignment of target and non-target model parameters to their associated category used to generate the *Viola guadalupensis* habitat model in the Guadalupe Mountains National Park. The desired model parameters of categories 1 through 6 included slopes >70%, aspects between 300 and 330°, and elevations >8,000 ft, respectively. Non-target parameters of Category 0 included all criteria outside the desired parameters. Category 6 was used to identify potential *V. guadalupensis* habitats throughout the park.

Category	Model parameters
0	Non-target parameters
1	Slope
2	Aspect
3	Elevation or slope and aspect
4	Elevation and slope
5	Elevation and aspect
6	Elevation, slope, and aspect

steep drainage. The ambient temperature was physically cooler in the early and late afternoon (1120 h and 1619 h). This rock wall faces north to northwest with a number of crevices and associated vegetation similar to VIGU1. The location is approximately 15 to 20 m long and 5 to 8 m tall with an elevation of approximately 2,500 m.

The second potential site (BMD2) possessed very tall and wide north- and west-facing cliff walls that appeared to be suitable habitat, however, as investigation of the area progressed into the afternoon (1300 h), the rock walls were observed to be more exposed to direct sunlight than earlier that morning (1100 h) as a result of sparse canopy cover. However, one rock wall, in particular, was considered suitable because it met all desirable criteria outlined by the model and remained shaded by *Pseudotsuga menziesii* and *Quercus* sp. at the time of investigation.

Finally, the third potential site near South McKittrick Canyon (SMK) possessed a number of small rock walls (between 3 × 3 m and 5 × 5 m) with one single location (designated SMK2) significantly shaded by *Ostrya knowltonii*, *Pinus ponderosa*, *Pinus strobiformis*, and *Pseudotsuga menziesii*. Data loggers, programmed to record light intensity, relative humidity, and temperature, were placed at VIGU1, VIGU2, WGP1, BMD2, and SMK2 for future comparison of microclimate data.

DISCUSSION

Significance of GIS-based predictive modeling.—The results of this study indicate two essential aspects for understanding the significance of this predictive model when compared to previous ground surveys and the habitat requirements of *V. guadalupensis*. First, the GIS-based habitat model located the type locality and an additional population of *V. guadalupensis* along Frijole Ridge, as well as three potentially suitable habitats for introduction west of this region. Since its discovery in 1990, extensive ground surveys of seemingly suitable habitat have been unable to locate additional populations (Powell & Wauer 1990). Based on our results, this study supports the relative usefulness of GIS-based habitat models for predicting the distribution of rare species consequently decreasing the ineffectiveness of random surveys.

Second, *V. guadalupensis* displays an affinity towards steep slopes, northerly aspects, and high elevations on Frijole Ridge. These results substantiate our assumptions that *V. guadalupensis* have specific topographic habitat preferences toward the variables used to develop our model. It is important to consider the fact that violets at VIGU2 were positioned on a northeast aspect rather than a northwestern aspect characteristic of VIGU1. This observation might indicate that aspects ranging from 300 to 45 degrees (northwest to northeast) may be a better representation of this species' aspect preference than those strictly between 300 and 330 degrees.

Model efficacy.—Considering two out of the nine predicted locations represented violet populations, while the remaining seven did not, suggests that 1) the variables used to develop the model were not specific enough to locate habitats strictly containing *V. guadalupensis* or 2) *V. guadalupensis* is restricted only to

these two locations on Frijole ridge and may have not had the opportunity to disperse to other areas. It is also important to take into account that three of the five locations not ground-truthed in this study were also located along Frijole Ridge. It is possible these locations may possess populations of *V. guadalupensis*. Further investigation into these areas is suggested in order to allow for a more complete model evaluation and to confirm the distribution of *V. guadalupensis* using this GIS-based habitat model.

Because the efficacy of a predictive model is dependant on the variables used to generate it, accurate information of habitat requirements for a species is necessary for the development of an accurate predictive model. Cherrill et al. (1995) stated that the rarity of a species greatly affects a model's efficacy to predict species-habitat distributions. Their model was generated from variables of known locations to predict rare and common species compared to traditional field surveys. Their results found a higher rate of accuracy for predicting common species than those of rare species. These results were dependent on the amount of information available for each species (Cherrill et al. 1995). Additional species-habitat information of *V. guadalupensis* (e.g., microhabitat conditions) will likely enable resource managers to generate a more effective model for predicting *V. guadalupensis* distribution and abundance.

Conservation and management.—Proper management of the two *V. guadalupensis* sites is vital for its continued existence within the Guadalupe Mountains. The distance between VIGU1 and VIGU2 (2 km) suggests that gene flow between these populations is unlikely. Because the most promising mechanism of seed dispersal across such distances is wind (Davies et al. 2004), this mechanism is improbable due to the density of vegetation around VIGU1 and the steep, narrow, rock walls surrounding VIGU2. These conditions likely protect these areas from wind rather than contribute to the use of wind-based seed dispersal. Consequently, understanding seed dispersal and genetic diversity between these two populations is essential for its conservation. Additionally, we suggest that introduction of violets into additional areas should include representatives from both locations to improve genetic diversity within new areas to prevent an additional bottleneck effect.

Although the locations of this species are far from human impact, several environmental factors may threaten the persistence of these populations. The accumulation of ladder fuels within the park has created conditions suitable for catastrophic wildfires along the East Rim. This could result in the burning of *V. guadalupensis* habitat or a reduction in the number of shade trees surrounding the area causing fatal heat temperatures from exposure (F. Armstrong, unpubl. report). Predation of leafs and seedpods by small mammals has been hypothesized to occur at VIGU1 (F. Armstrong 2002 and 2004, unpubl. field notes). Even though there has been no direct observation of this activity, seed predation will likely affect the reproductive success of individual plants, reducing overall genetic diversity and dispersal.

Continued monitoring of both *V. guadalupensis* sites and comparing the long-term microhabitat conditions of known violet sites to potential introduction sites will provide a better understanding of specific habitat requirements for introduction and habitat management. The two populations of violets, as well as the three uninvestigated sites on Frijole Ridge, should also be considered during fire management planning to prevent unfavorable conditions due to catastrophic wildfires along the East Rim.

The habitat model developed by the National Park Service to predict potential *V. guadalupensis* habitat has provided critical baseline data for additional investigations and research within GMNP. Due to the success of finding an additional population and other suitable sites for introduction, resource managers can utilize this information for continuing plans to proliferate and conserve *V. guadalupensis* populations with potential success.

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ANNOTATED VASCULAR FLORA OF THE DEAD HORSE MOUNTAINS, BIG BEND NATIONAL PARK, TEXAS, WITH NOTES ON LOCAL VEGETATION COMMUNITIES AND REGIONAL FLORISTIC RELATIONSHIPS

Joselyn Fenstermacher
Sul Ross State University
Box C-64
Alpine, Texas 79832-0001, U.S.A.
jfen158@sulross.edu

A. Michael Powell
Sul Ross State University
Box C-64.
Alpine, Texas 79832-0001, U.S.A

Joe Sirotnak
P.O. Box 29
Box C-64
Big Bend National Park, Texas 79834-0029, U.S.A.

Martin Terry
Sul Ross State University
Box C-64
Alpine, Texas 79832-0001, U.S.A.

ABSTRACT

The Dead Horse Mountains of Big Bend National Park are one of the least explored areas in Texas. This is the first collective body of work to document the area's vascular flora through a major new collection of vouchered specimens and a survey of existing herbarium specimens. Field work was performed between August 2003 and September 2006. The study area covers 176,800 acres (71,548 hectares; 276 mi², 715 km²) with a 4100 ft (1250 m) range in elevation. Non-vascular specimens (bryophytes, hepatophytes, and lichens) were also collected but not included in the final analysis. A total of 1584 vascular specimens were collected during the current study; a herbaria search uncovered 2212 previously-collected vouchers. The flora consists of 662 species in 344 genera and 91 families. The best-represented families are the Asteraceae (80 species), Poaceae (75 species), Fabaceae (52 species), Euphorbiaceae (34 species), Cactaceae (34 species), Pteridaceae (20 species), and Boraginaceae (20 species). *Seymeria falcata* var. *falcata* was collected for the first time in the United States while eight new species were recorded for Brewster County. One additional taxon (*Galactia* sp.) may be undescribed or new to the United States. Vouchered taxa increased by 12% and 55 species were documented in the study area for the first time. Twenty-four non-native species are known from the study area; three are state-listed noxious weeds, and six are considered invasive. The number of known Texas endemics in the Dead Horse increased to 11; seventeen species are considered rare. The Dead Horse flora differs from other southwestern floras mainly by an increased relative importance of monocots, and the elevation of the Poaceae to be co-dominant with the Asteraceae. These and other factors suggest connections to several peripheral floristic areas, ranging from the Mogollon Rim and the Great Plains to South Texas and southern Mexico.

RESUMEN

La Sierra del Caballo Muerto del Big Bend National Park es una de las zonas menos exploradas en Tejas. Este es la primera investigación que documenta la flora vascular de esta zona mediante una colección importante de especímenes nuevos y un examen de los especímenes existentes en herbarios regionales. La investigación fue realizada entre Agosto 2003 y Septiembre 2006. La zona de la investigación cubre 176.800 acres (71.548 hectáreas; 276 mi², 715 km²) con una gama de 4100 pies (1250 m) de elevación. Especímenes de plantas no vasculares se recogieron pero no fueron incluidos en el análisis final. Durante el estudio actual, se recogieron unos 1584 especímenes de plantas vasculares; en la búsqueda de herbarios se encontraron 2212 especímenes recogidos anteriormente. La flora final consiste en 662 especies de 344 géneros y 91 familias. Las familias mejor representadas fueron las Asteraceae (80 especies), Poaceae (75 especies), Fabaceae (52 especies), Euphorbiaceae (34 especies), Cactaceae (34 especies), Pteridaceae (20 especies), y Boraginaceae (20 especies). *Seymeria falcata* var. *falcata* fue recogida por primera vez en los Estados Unidos, y fueron registradas ocho nuevas especies para el condado de Brewster. Una colección adicional (*Galactia* sp.) puede ser una especie nueva o una especie desconocida en los E.U. El número de taxa con especímenes documentadas creció en un 12%, y 55 especies fueron documentadas en la zona del estudio por primera vez. Se reconocen 24 especies exóticas en la zona del estudio; nueve se consideran plantas invasoras o hierbas nocivas. El número de especies endémicas de Tejas que se han encontrado en la Sierra Caballo Muerto subió a 11; diecisiete especies se consideran raras. La flora de la Sierra del Caballo Muerto se distingue de otras floras del sudoeste de los E.U. principalmente por el incremento en la importancia relativa de las Monocotiledóneas, y por la elevación de las Poaceae hasta el punto de ser co-dominantes con las Asteraceae. Estos y otros factores sugieren que existen conexiones con varias áreas florísticas periféricas, extendiéndose desde el Mogollon Rim en Arizona y los Grandes Llanos de los E.U., hasta el sur de Tejas y México meridional.

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INTRODUCTION

The Dead Horse Mountains (DH) of Big Bend National Park (BBNP) create a remote and forbidding viewscape on the West Texas park's eastern skyline (Fig. 1). The rugged limestone escarpments offer no reliable surface water, nor infrastructure allowing quick access to the interior, leading to claims of it as being uncharted wilderness (Wood et al. 1999). These logistical challenges, in addition to rugged topography and extreme climate, have left the area one of the least botanically understood areas in Texas and the northern Chihuahuan Desert Region (CDR). Much collecting has taken place in the area over the past 100 years. The height of early scholarly investigations came in the 1950s–1960s, and included a SRSU master's thesis by Rogers (1964), a short but excellently characterized field report by Wells (1965), and collections by numerous professionals including Sul Ross State University (SRSU) botanist Barton Warnock. The largest coherent body of collections was made for a report to the Nature Conservancy (Amos and Giles 1992), which at the time owned a part of the study area that is now part of the Texas Parks and Wildlife's Black Gap Wildlife Management Area.

The majority of vouchers made through these efforts came from more easily-accessible areas, near roads and trails peripheral to the heart of the range, without widely sampling the range of niche habitats existing in the area. Despite a rather active historical interest in this area, no overall floristic characterization has been made for the Dead Horse. Several lists of local flora exist, including more than one in use for Big Bend National Park; however these are based on sightings, literature reports and, to an unknown degree, herbarium specimens (Mahler 1971; National Park Service 1996; Louie 1996; Clelland 2001; Worthington 2001; Alex et al. 2006).

A floristic analysis of the Dead Horse will create an important context for Big Bend regional floristics. The DH are located in the Trans-Pecos Mountains and Basins vegetational area (Hatch et al. 1990) but phytogeographic connections have been noted with other Texas floristic areas including the High Plains, Rolling Plains, Edwards Plateau, and the South Texas Plains, also known as the Tamaulipan Thornscrub region (Powell 2000). Connections to more northerly vegetational areas are evidenced by the populations of aspen (*Populus tremuloides*), Douglas-fir (*Pseudotsuga menziesii*), and other Rocky Mountain species growing well south of their normal distributions. Floristic links also reach south to the Sierra Madre Oriental and Occidental, expanding to the greater CDR of Mexico (Larke 1989). The graminoid flora even has an affinity to the Great Plains grasslands (Powell 2000; Christie 2006). Because there are so many regions intergrading in the local area, there is high potential in the study area to discover species out of their expected ranges. Furthermore, the DH is topographically complex and the resulting microclimates may harbor species new to science. Already the area shelters several little-known species: *Andrachne arida* is known from only a few localities in the CDR and has not been seen in the DH since the 1960s, while the purported Dead Horse endemic *Hedyotis pooleana* has not been observed since the original 1985 collection. Other species are assumed to occur in the study area based on their known habitat, but are not well understood, being known only from a few collections in a restricted area. One such example is *Bouteloua kayi;* previous to this study it was not known to occur in the study area but was discovered during the current work.

The environmental complexity, in both topography and regional climate regimes, no doubt has helped to produce the numerous endemic species of the CDR, but instead of being widespread, endemics are mostly locally distributed (Brown 1994). Indeed, in Trans-Pecos Texas, Brewster County tallies the highest numbers of endemic (TAM-BWG 2007) and rare plant species (Alex et al. 2006; Poole et al. 2007). Often, however, species of concern are little known beyond data taken at their original collection site. Thus, targeted field studies in Chihuahuan Desert areas like the Dead Horse have a high potential for new floristic discoveries.

The main objective of this project was to create a collective body of work describing the floral composition of the DH. Goals to accomplish this objective included: (1) developing an annotated flora for the study area through documenting existing voucher specimens in regional herbaria, and through new collections from a wide variety of underrepresented areas and habitat niches in the range; (2) gaining more knowledge about little-known species that occur in the range, including species known regionally but not yet recorded

Fig. 1. The Dead Horse Mountains study area. Western slopes of central portion of the range, with Sue Peaks at left of center.

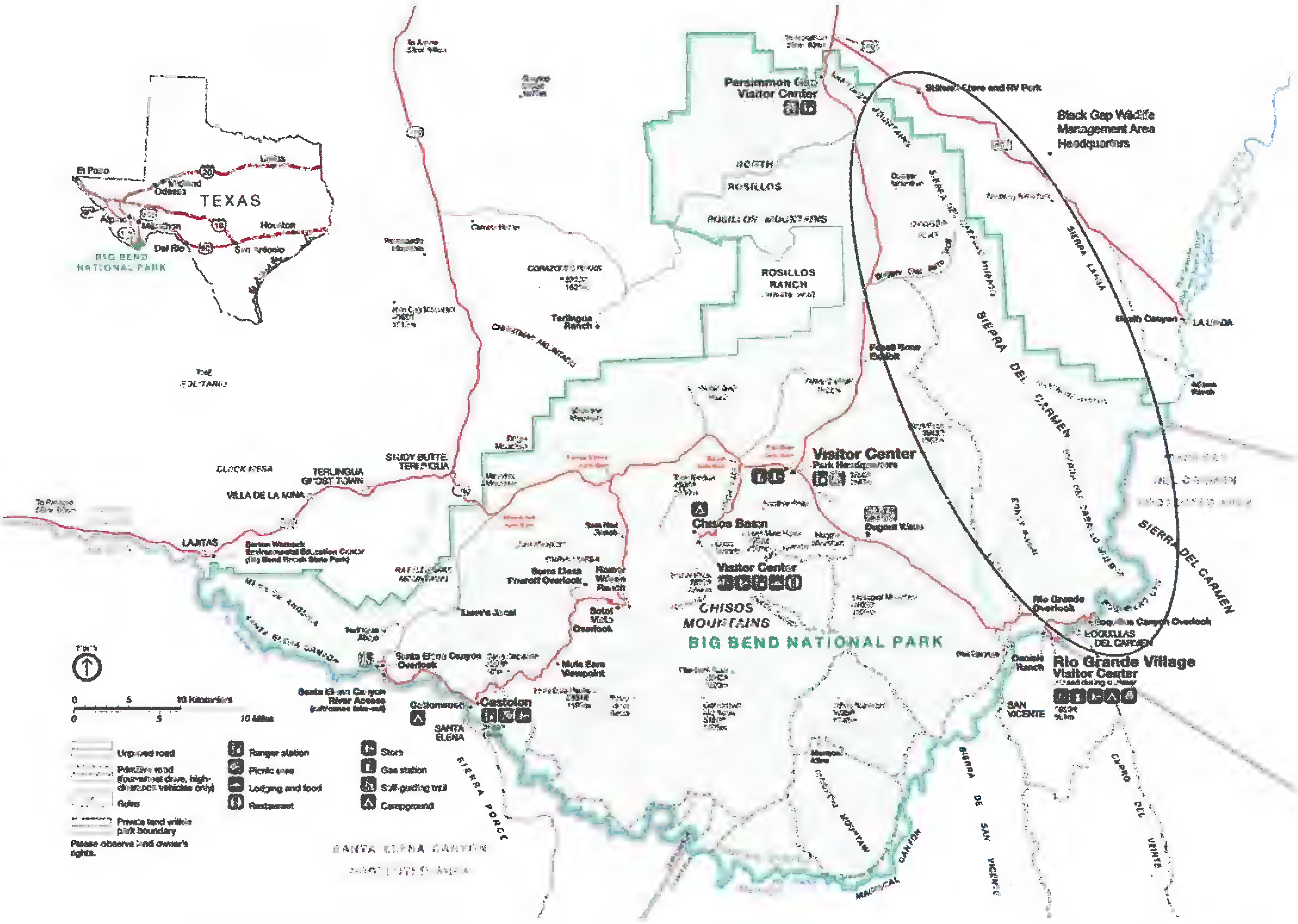

Fig. 2. Map of Big Bend National Park (NPS 2004) with the study area circled. The Dead Horse Mountains are labeled "Sierra del Carmen" and "Sierra del Caballo Muerto."

within the study area; and (3) documenting the occurrence of novel species for the study area, whether rare, disjunct, or invasive, and providing new insight into their distributions and habitat requirements. Subsequent analysis was used to interpret the Dead Horse flora in a larger regional context within the Trans-Pecos and also the larger southwestern United States. The study was conducted as the first author's MS thesis research (Fenstermacher 2007). The full thesis manuscript, the entire voucher collection database, and many related photos can be found on the Cactus Conservation Institute, Inc. website: http://www.cactusconservation.org/CCI/botany/fdhm.html.

Site Description

The DH are located in the Big Bend region of western Texas, in southern Brewster County about 80 mi south of the town of Alpine (Figs. 1, 2). The study area boundary starts in the northeastern part of the national park at Dog Canyon, continues south along the western foothills of the DH, and extends east into a portion of Texas Parks and Wildlife's Black Gap Wildlife Management Area (BGWMA), including a few parcels of private ranchland (Fig. 3). The Rio Grande marks the southern limit. The DH are a smaller, northern extension of the impressive Sierra del Carmen of northern Mexico, exhibiting similar physical characteristics: northwest-trending ridges alternating with alluvial basins, and generally rugged, arid, rocky terrain. Extending 31.5 mi (51 km) N/S and an average of 8.5 mi (14 km) E/W, the study area covers approximately 176,800 acres (71,548 ha; 276 mi^2, 715 km^2), and ranges in elevation from 1800 ft (549 m) at the Rio Grande to 5840 ft (1780 m) at Sue Peaks in the heart of the range.

The only major physical feature that trends east-west in the study area besides Boquillas Canyon along the Rio Grande is the 14-mile-long (22.5 km) Telephone Canyon that bisects the DH. There are several major drainages in the study area, but there is no permanent surface moisture. Any precipitation that occurs usually flows overland into the dry arroyos, creating powerful but temporary floods draining towards the Rio Grande. Away from the river, surface water is found only unreliably in tinajas, i.e., stone basins eroded usually out of arroyo or canyon beds with bedrock outcrops. The study area experiences hot summers and cool-to-cold winters. The average annual high is 85°F while the low averages 53°F with an average annual maximum of 100° F/38° C and minimum of 33° F/1° C. Large diurnal temperature ranges are common, with a mean of about 32° F/0° C and a maximum of about 50° F/10° C. Precipitation peaks between May and October, the 10 in/25 cm yearly average falling usually as late afternoon thunderstorms that range in intensity and often create hail (temperature data from National Park Service, Big Bend National Park, unpublished data).

The DH are composed primarily of lower Cretaceous limestone deposited in a deep sea environment ca. 180 mya. As the area was close to the shoreline of the great interior sea, and as sea levels fluctuated, some shales and clays were deposited, reflecting the changing environment. During the Cenozoic (ca. 30 mya), massive blocks of Del Carmen and Santa Elena Limestone were uplifted and tilted along fault lines, resulting in the basin and range morphology seen today: gradual western slopes and steeper escarpments to the east, alternating with alluvial basins in between (Maxwell 1979). DH soils are mostly shallow with a high percentage of rock fragments (mostly calcium carbonate). Rock outcrops are frequent and most slopes are steep. There are small, localized areas on alluvial uplands where the soils are slightly deeper, while deep, loamy soils can be found in some basins and near the Rio Grande. The highest elevations have soil darker in color because of its high organic content and may be moist more often than dry (Cochran & Rives 1985).

Human History and Disturbance Regimes

People were living in the Big Bend area as early as the late Paleo-Indian period (12,000–6500 BC) and there is abundant evidence of habitation in the Dead Horse dating from the Archaic period (6500 BC–ca. 100 AD; Alex 1990). The periphery of the DH was most probably used as a travel corridor throughout history until more permanent settlement occurred in the Historic era (1535 AD– present); after the threat from hostile Indians was removed, ranching and mining activities increased substantially (Tyler 1975).

Human-induced disturbance regimes that have affected DH to a small degree include grazing, natural-resource harvesting of *Euphorbia antisyphilitica* and *Bouteloua ramosa*, infrastructure developments related to cinnabar ore mining, fire, and recreational pursuits such as hiking, camping, and river rafting. However, the

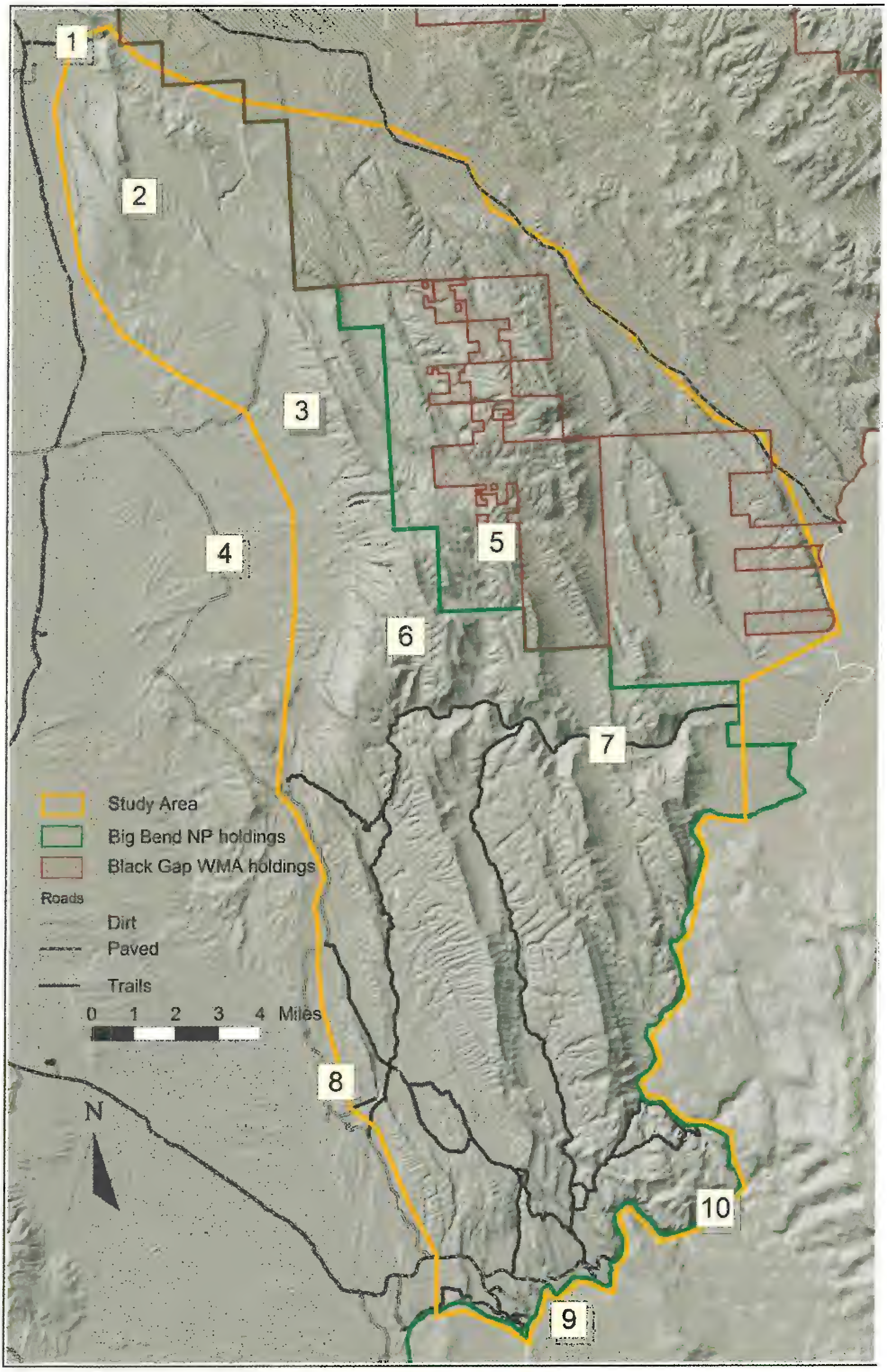

Fig. 3. Dead Horse Mountains study area locations: (1) Dog Canyon, (2) Dagger Mountain, (3) Stuarts Peak, (4) Old Ore Road, (5) Brushy Canyon, (6) Sue Peaks, (7) Telephone Canyon, (8) Ernst Tinaja, (9) RGV, (10) Boquillas Canyon.

Fig. 4a–b. Examples of different vegetation zones within the Dead Horse Mountains study area. A. Mixed Desert Scrub (dsc), lower Telephone Canyon trail area. B. Sotol-Yucca Grassland (syg), upper Telephone Canyon trail area.

Fig. 4c–d. Examples of different vegetation zones within the Dead Horse Mountains study area. C. Chaparral (chp), above Brushy Canyon. D. Desert Canyon (dca), east of Dagger Mountain.

Fig. 4e–f. Examples of different vegetation zones within the Dead Horse Mountains study area. E. Rio Grande Riparian Corridor (rio), Boquillas Canyon. F. Mixed Desert Scrub and Sotol-Yucca Grassland, Stuarts Peak.

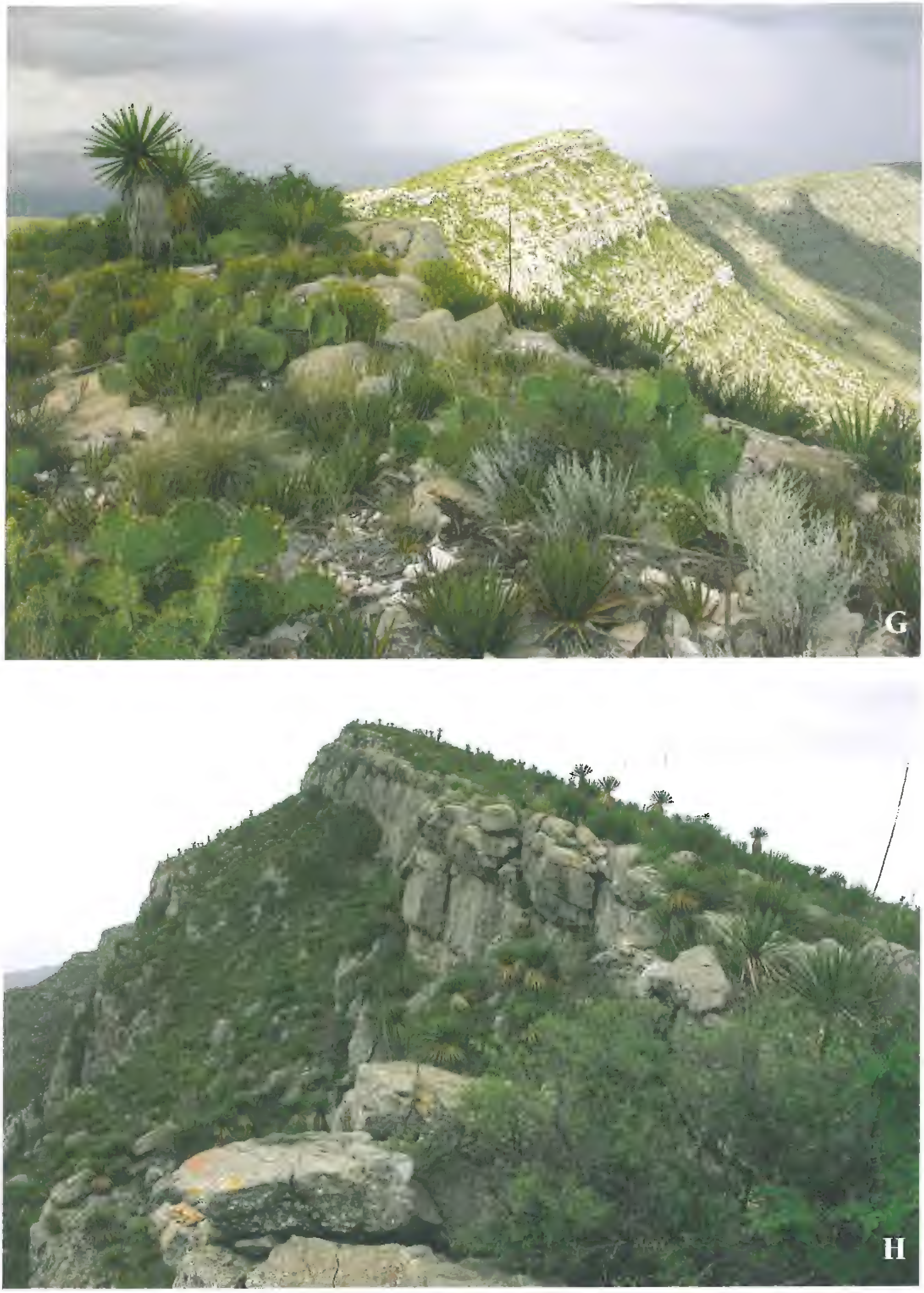

Fig. 4g–h. Examples of different vegetation zones within the Dead Horse Mountains study area. G. Sotol-Yucca Grassland, Sue Peaks. H. Chaparral, Sue Peaks.

most damaging and far-reaching would likely be the increased distribution and dominance of invasive plant species. *Tamarix* spp. and *Arundo donax* have expanded their range along the Rio Grande, creating miles and miles of dense thickets lining the riverbanks. *Pennisetum ciliare* is well established in the lower elevations of BBNP, including the extreme southern end of the study area. However, it is not as dense as it has become in other low-elevation areas, perhaps being held in check by other non-native species, burros and horses. The livestock enter the park from Mexico, trampling vegetation and breaking up biological crusts, increasing the erosion potential in many places along the river corridor.

Fire may be a significant natural factor driving the study area ecology, creating the characteristic patchiness of higher elevation vegetation. Human-caused fires are limited to the developed areas but the interior burns are mainly lightning strikes, burning an individual yucca in more barren rocky areas, but sometimes being carried through drainages or at higher elevations where the biomass is denser. Henrickson and Johnston (1986) suggest that the unique Yucca Woodland community at higher CDR elevations may be maintained by fire, favoring the semi-succulent monocots over more woody species. There has been little suppression effort in the DH, so current states should be considered normal.

General Vegetation Description

Many workers have proposed vegetation classification systems relevant to the region. For the CDR as a whole, there exist excellent overviews of basic and detailed vegetation structure (Morafka 1977; Henrickson & Johnston 1986, 2004; Brown 1994; Powell & Hilsenbeck 1995). Descriptions in several local floras (Rogers 1964; Butterwick & Strong 1976; Amos & Giles 1992; Hardy 1997) demonstrate the degree of local diversity possible within hierarchies created by the above publications. Beyond a large-scale tendency towards homogeneity (Brown 1994), the DH and larger CDR have basic plant-community types that intergrade and change in abundance and dominance in response to the complex physiography. Perhaps Whittaker, as quoted in Takhtajan (1986), has offered the best explanation for general Chihuahuan Desert vegetation patterns: in warm, semi-arid deserts there is no clear convergence of dominant forms as can be found in cool semi-deserts. Warm deserts may be too dry to support arborescent life-forms or consistent canopy cover. However a diversity of non-arborescent growth is supported in pockets of higher moisture availability, maintained by the right combination of aspect, slope, elevation, and substrate. Larger plants, such as shrubs and *Yucca* spp., can also create special microclimates. Many species take advantage of the shade and wind protection that these larger nurse plants provide. This could be considered the canopy of the CDR—low and discontinuous, but functional.

Two vegetation maps, produced through remote sensing and some vegetation sampling, generally include the study area (Plumb 1991, 1992; Wood et al. 1999) but are limited by inadequate sampling and ground-truthing. However they are useful to form an overall impression of the relative importance of cover types. Based on a consolidated version of Plumb's (1991, 1992) vegetation maps, Lechuguilla Scrub covers 50.4% of the study area. This vegetation type includes *Agave lechuguilla*, *Opuntia* spp., *Euphorbia antisyphilitica*, and many species of grasses. Almost equally important in the study area is the High Desert Grassland vegetation at 45.1% coverage, where species like *Nolina erumpens*, *Dasylirion leiophyllum* and *Yucca* spp. are codominant with graminoids.

METHODS

The herbaria of institutions that sponsored botanists known to collect in the Big Bend, in addition to those geographically close to the study area, were contacted and when possible electronically searched: Angelo State University (SAT), the Botanical Research Institute of Texas (BRIT), the New York Botanical Garden (NYBG), Sam Houston State University (SHST), Sul Ross State University (SRSC), the Texas A&M University Biology Department herbarium (TAMU), Texas A&M's Tracy herbarium (TAES), Texas State University (SWT), University of Kansas (KANU), University of Texas at Austin (TEX-LL), the University of Texas at El Paso (UTEP), and Big Bend National Park (BIBE). Sheet-by-sheet searches were conducted at SRSC and BGWMA.

All species found in flower were collected during every trip. Collection of rare species or plants of uncertain identity and/or distribution was guided by BBNP protocol: no more than 10% of the individuals of any viable reproductive population of a rare plant were harvested. Most collecting was done within the National Park, due to easier and quicker access to more areas. Access to the study area was mainly on foot using cross-country navigation but two rough dirt roads and two maintained trails did provide effective access to more interior areas of the range. Two river trips allowed limited southern access. A few extended, overnight trips were enabled by water caches previously transported into the backcountry by NPS trail crew personnel and packstock.

Sampling areas were chosen based on intricacy of topography such as deep and/or sinuous canyons, unvisited but potentially unique areas such as the higher peaks, and otherwise intriguing spots identified on USGS 1:24,000 topographic maps. Search methodology was a directed meander (Goff et al. 1982) at each locality visited, focusing on promising microhabitats and moving from patch to patch as the observable species diversity was documented. Field notes and resulting label data included collection location, habitat, habit, description of notable plant features, relative abundance, and associated species. UTM coordinates were taken on site or approximated post-field using digital elevation model data through ArcView 3.2. Specimens were identified using multiple sources, including Correll and Johnston (1970), Warnock (1970, 1974, 1977), *Flora of North America* Poaceae and Asteraceae volumes (FNA 2003b, 2006, 2007), Powell (1998, 2000), Yarborough and Powell (2002), Turner et al. (2003), and Powell and Weedin (2004). Specimens were determined by B.L. Turner of TEX-LL and A. Michael Powell of SRSC. The atlas of Turner et al. (2003) was the primary source for nomenclature and distributional data, and two online sources (ITIS 2007, MBG 2007) were followed for author information. The *Manual of the Vascular Plants of Texas* (Correll & Johnston 1970) provided the fundamental taxonomic guidelines for this work. However, numerous other sources were utilized for the most up-to-date taxonomic interpretations, most notably Powell (in prep.) and Powell et al. (in ms.) for non-woody vascular species and genera, the *Flora of North America* for Poaceae and Asteraceae treatments (FNA 2003b, 2006, 2007), and Powell and Weedin (2004) for the Cactaceae. Voucher specimens made during this project were deposited at SRSC; selected duplicates were sent to BIBE, TEX-LL, and BRIT.

RESULTS AND DISCUSSION

Between August 2003 and September 2006, a total of 49 days and approximately 400 hours were spent in the field. The 1549 voucher collections made during those three years, plus four observations without vouchers, represent 84 families, 283 genera, and 490 species, totaling 493 taxa at or below the species level. The herbaria search revealed an additional seven families, 58 genera, and 173 species (178 taxa) that were not encountered during the current study. Similarly, the current study documented an additional seven families, 45 genera, and 120 species (121 taxa) beyond the historical baseline found in the herbaria search. Fifty-five of those additional 120 species were new records for the DH, representing a 10% increase in known taxa. Another 65 species (67 taxa), though not previously represented by vouchers, were common and suspected to occur and thus not considered novel records. In sum, the total known flora of the DH to date consists of 91 families, 344 genera, and 662 species (671 total taxa).

The Asteraceae is the most prominent family in the DH, tallying 80 species. Other important families include the Poaceae (75 species), Fabaceae (52 species), Euphorbiaceae (34 species), and Cactaceae (31 species). The eight most species-rich families comprise 50% of the flora while 24 families are represented by a single taxon. The most abundant genera represented in the DH are *Chamaesyce* and *Dalea* at 13 species each.

A taxonomic breakdown of species found in the DH shows that eudicots make up the largest proportion of the flora at 78.9% (Table 1). Gymnosperms comprise the smallest portion of the flora after monocots and the ferns and fern allies. Perennial herbs were the most abundant life form encountered, followed by annual herbs, shrubs, subshrubs, succulents, vines, and trees (Table 2). The annotated list of species found in the DH provides the following information for each taxon: native status, new records, rare species status

Table 1. Taxonomic composition of the flora of the Dead Horse Mountains.

Taxonomic group	Families	Genera	Species Native	Non-native	Total Species
Ferns and fern allies	3	7	23	0	23
Gymnosperms	3	3	7	0	7
Monocotyledons	10	57	100	7	107
Eudicotyledons	75	277	508	17	525
Totals	**91**	**345**	**638**	**24**	**662**

Table 2. Summary of the Dead Horse Mountain flora by life form (USDA 2007). The semi-succulent members of the Agavaceae, Liliaceae, and Bromeliaceae were included in the shrub category. Eight taxa can be either trees or shrubs depending on the habitat. These were divided equally between the tree and shrub categories. Twenty-eight taxa were listed by USDA as both annual and perennial herbs. These were split evenly between the two herb categories. Graminoid species were included under herbs.

Life Form Species	Number of of Flora	Percent
Trees	27	4.1
Shrubs and semi-succulents	97	14.7
Sub-shrubs	55	8.3
Vines	29	4.4
Annual herbaceous	1	0.2
Perennial herbaceous	24	3.6
Woody	4	0.6
Herbs	420	63.4
Perennial	277	41.8
Annual	143	21.6
Cacti and succulents	34	5.1

and ranking, common name, selected synonyms, relative abundance in the study area, life form, vegetation community, elevation, and all known vouchers.

Herbarium search

It is certain that more DH collections exist in regional herbaria. The collections of one botanist who made significant collections in the BGWMA reside at BRIT, but are not electronically databased. Unfortunately, time and funding constraints precluded a sheet-by-sheet search of that institution for this project. Digital records are a boon to this type of research; however, when in existence they should not be assumed to be complete or entirely accurate. For example, in researching the holdings at SAT, an online search of the Floral Consortium of Texas website revealed 64 vouchers, but an onsite search of SAT's internal digital database resulted in 245 collections, with only three overlapping with the consortium's results. Added to that discrepancy is the fact that not all of the holdings at TEX-LL are included in their online searchable database. Given that that is the main repository in the state, there is a high probability that many DH vouchers were not accounted for through the herbaria search.

Completeness

In the entire history of collection efforts in the study area, including those during the past 15 years, there was a significant rise in species found, without any evident leveling of return for effort. This is to be expected, with much new territory having been covered in more recent years by the Amos survey of Brushy Canyon in addition to the current project. However, the return of new species per year of effort during the course of this study began to taper off and fewer new species were found than remained unseen from the historical

baseline. Some historically collected areas were not revisited, such as the more inland riparian habitats of the Rio Grande Village area, where species may still be extant or perhaps extirpated due to the changing nature of the river corridor. More localized examination of return for effort tells a mixed story: after three visits to the same area of mixed, mid-elevation habitat, there was no reduction of return for effort. However, after two trips to the high-elevation Sue Peaks environment, the return of new species decreased by about 50%. The differences may lie in the types of habitat visited, but one must also keep in mind the vagaries of desert flora—life strategies built around responses to ephemeral rain, general seasonal/temperature restrictions, and even biennial cycles, all serve to limit the flora present at any given time. Certainly more species await documentation in the study area; collections were made throughout most of the Dead Horse range, but some interior locations such as Margaret Basin, the upper Strawhouse trail, the eastern end of Telephone Canyon, and areas interior to Boquillas Canyon remain under collected. Despite this, however, it seems clear that the majority of the flora has been documented.

Vegetation Patterns

Henrickson and Johnston (1986) comment on the high degree of intergradation between vegetation types in the CDR and the difficulty of placing many areas into an exact classification. This can result in many sub-types being recognized, as in their and Plumb's (1992) work. In the DH, six vegetation types are clearly distinguishable, separated generally by elevation and water availability. These types are similar to ones identified by Henrickson and Johnston for the CDR. Other CDR types may have only marginal representation in the DH and are discussed as unique habitat areas. The three dominant types follow elevational zones, with Mixed Desert Scrub (DSC) at lower to mid elevations (Figs. 4a, f), Sotol-Yucca Grassland (SYG) at mid-to-high elevations (Figs. 4b, f, g), and Chaparral (CHP) appearing in patches at the highest elevations within the SYG (Figs. 4c, h). The remaining three vegetation types involve riparian-related areas, including arroyos, canyons, and the Rio Grande corridor. The Sandy Desert Arroyo (DAR) and Desert Canyon (DCA) types interlace with and intersect mainly the lower elevations of DSC but can allow intermixing of higher- and lower-elevation species in steep, protected drainages on mountain slopes (Fig. 4d). The Rio Grande Riparian Corridor (RIO) is the only vegetation type that occurs in association with permanently flowing water and mainly occurs within Boquillas Canyon (Fig. 4e), although the slightly inland, developed areas around RGV have significant riparian habitats that are important to the diversity of the study area. Although few plants are seen throughout the range at all elevations, *Agave lechuguilla* and *Aristida* spp. are possibly the most ubiquitous.

Mixed Desert Scrub.—The DSC vegetation type extends from the lowest elevations to about 4000 ft (1220 m), nearing the higher plateaus of the Dead Horse. The lowest elevations and flattest terrain of the park are dominated by *Larrea tridentata*, which is seen most often on low, foothill approaches and interior basins of the DH. Intermingling at lower elevations are *Opuntia aggeria* and *O. grahamii, Parthenium incanum, Nama hispidum,* and *Acacia neovernicosa. Flourensia cernua* is often cited as being important, even co-dominant, in this ecological zone of the CDR, but it was rarely seen. Moving upslope, various shrubs, succulents, and grasses become more important. Species commonly encountered and expected include: *Tiquilia greggii, Prosopis glandulosa, Condalia* sp., *Ziziphus obtusifolia, Buddleja marrubiifolia, Leucophyllum minus* and *L. candidum, Viguiera stenoloba*, and *Chrysactinia mexicana*. Intergrading with lower-elevation species is *Dasylirion leiophyllum*, which begins to occur as low as 3500 ft (1066 m), but extends to the highest elevations of the range. Dense stands of the rhizomatous *Agave lechuguilla* and *Hectia texensis* occur sporadically and usually include more obvious occurrences of the following common species: *Selaginella lepidophylla, Selaginella wrightii, Astrolepis* spp., *Argyrochosma microphylla, Calliandra iselyi*, and *Opuntia rufida*. Biological soil crusts of varying degrees of development occur in most inter-rock spaces, harboring various species of cyanobacteria, lichens, and in the right environment even mosses.

Desert Arroyo.—Many of the general DSC species overlap into the dry watercourses intersecting the region; the two xeric-riparian vegetation types are generally distinguishable according to the amount of moisture available. DAR, or Sandy Arroyo Scrub as named by Henrickson and Johnston (1986), occurs in more open, low-elevation drainages incised into the desert flats. The margins are rich with perennial plants, which

often grow into impenetrable thorny thickets across the wash. *Fallugia paradoxa* and *Brickellia laciniata* are commonly present in the wash cobbles of larger drainages, while *Prosopis glandulosa, Guaiacum angustifolium, Forestiera angustifolia, Celtis pallida, Lycium berlandieri,* and *Porophyllum scoparium* are common throughout.

Desert Canyon.—In rockier habitats, larger drainages, and within canyons that provide partial shade, the DCA vegetation type includes additional species such as *Berberis trifoliolata, Fraxinus greggii, Diospyros texana, Eysenhardtia texana, Lippia graveolens, Mimosa* spp., *Acacia roemeriana, Schaefferia cuneifolia, Rhus virens, Tecoma stans, Clematis drummondii, Passiflora tenuiloba,* and *Maurandya antirrhiniflora*. Common wash-associate grasses are *Bothriochloa laguroides, Heteropogon contortus, Setaria leucopila,* and *Aristida* spp. More water-dependent species such as *Ungnadia speciosa* and *Chilopsis linearis* occur infrequently, restricted to the largest drainages.

Juglans microcarpa is not a typical DH species within BBNP; it was seen only once in the National Park at the north end of the range, but as reported by Amos and Giles (1992), it was observed during the current study to be much more dominant in BGWMA's Brushy Canyon. In the same Amos and Giles (1992) report, *Cercis canadensis* var. *mexicana* was listed as a dominant in Brushy Canyon; it was not observed in the National Park portion of the DH. Canyon walls throughout the range provide a relatively consistent but limited habitat for cliff-dwelling species including *Cirsium turneri, Perityle aglossa,* and *Perityle bisetosa* var. *scalaris*.

Rio Grande Riparian Corridor.—A more traditional riparian woodland vegetation type exists only along the Rio Grande, where the consistent water table can support native species such as *Populus fremontii, Salix* spp., *Baccharis salicifolia, Phragmites australis,* and the introduced and invasive *Arundo donax* and *Tamarix* spp. A few solitary individuals of more water-dependent genera (e.g., *Salix, Baccharis,* and *Tamarix*) occur in at least one other place in the DH interior: above Ernst Tinaja, where their water-hungry roots may have found a perched water table. Also important along the Rio Grande are *Acacia farnesiana, Nicotiana glauca, Prosopis glandulosa,* and *Chilopsis linearis*.

The major, non-native species have altered and will continue to alter the riparian landscape. Thickets of cane with abundantly dense rhizomes have solidified the river banks, channelizing the watercourse. This creates, in many cases, an irreversible cycle: the channel concentrates the river flow, which increases its velocity and thus erosive power, which, in turn, creates a deeper channel that does not allow flooding over its banks as easily as before. With over-bank flooding decreased due to channelization and a generally reduced flow/flood cycle due to upstream dams, dense canopies of *Arundo donax* and *Tamarix* spp. are allowed to establish, precluding the formation of native *Salix* spp. and *Populus* spp. bosques (Howe & Knopf 1991, Bell 1997).

Sotol-Yucca Grassland.—Found on the higher elevation slopes and plateaus to the highest peaks, SYG is the dominant vegetation above DSC. The vegetational boundary seems to occur, at least on the western side of the range, at around 5000 ft (1524 m), where the steep western slopes top out to form a main central plateau within the DH range. Stuarts Peak, though slightly lower at 4800 ft (1463 m), should also be included, due to its many unique floristic characteristics, including a diverse lichen flora and, in the DH, the only known populations of two species that are more expected in montane forested vegetation—*Philadelphus microphyllus* and *Achnatherum curvifolium*.

SYG is a visually distinct zone where large yuccas and sotol stand out from the shrub- and grass-dominated understory. Also known as Izotal, Sotolal, and Rosetófilo, this vegetation type is considered by some to be shrub-dominant (e.g., Henrickson & Johnston 1986), and so the term "grassland" is omitted in their official terminology. The DH do seem to have a persistent shrub component dominated by *Dasylirion leiophyllum, Nolina erumpens,* and *Yucca* spp., even as the grass diversity and abundance increase with elevation. However, the two life-forms seem to be codominant and the term "grassland" is used here to convey the importance of bunch grasses in the inter-shrub spaces. On the main DH plateau, *Nolina erumpens* becomes a significant, visual member of the SYG creating, along with the *Dasylirion leiophyllum*, large masses of thick vegetation, standing in some places almost head high.

Common plants associated with the SYG of the DH include *Yucca torreyi, Yucca thompsoniana, Nolina erumpens, Fouquieria splendens, Parthenium argentatum, Bouchea spathulata, Leucophyllum* spp., *Bernardia obovata, Vauquelinia angustifolia, Mortonia scabrella, Zinnia acerosa, Coryphantha tuberculosa* var. *tuberculosa, Coryphantha echinus, Neolloydia conoidea, Epithelantha macromeris, Bouteloua curtipendula, Aristida* spp., *Enneapogon desvauxii, Leptochloa dubia,* and *Muhlenbergia tenuifolia.*

True grasslands, though included in reviews of CDR vegetation types, are not functionally a part of the DH environment. Areas that are clearly dominated by graminoids without a significant shrub component are more commonly associated with the higher plains around the towns of Marathon, Alpine, and Marfa in the northern Big Bend. In the DH, grasses are important components of the shrubby slopes and higher plateaus, and at higher elevations, a few species that are important components of the vast grama grasslands to the north do occur. However, small areas dominated by grasses occur only on the scale of remnant patches rather than functional ecosystems; they are not dense or contiguous enough, nor dominated enough by the typical grassland species *Bouteloua eriopoda* and *Bouteloua gracilis*, to be considered a true grassland. This seems to follow a general trend of grama grasslands' being established on igneous soils, whereas limestone substrates in similar conditions will support only desert-scrub assemblages (Henrickson & Johnston 1986).

Chaparral.—Small pockets of shrub thickets, or CHP, occur within the SYG on plateaus and eastern slopes associated with the high elevations of the Sue Peaks area. Small and sometimes dense clumps of *Quercus pungens*, some *Quercus mohriana* and *Quercus grisea, Cercocarpus glaberoides, Berberis trifoliolata* and *Rhus virens* associate with large *Dasylirion leiophyllum* and *Nolina erumpens*, all overtopped by the occasional but conspicuous *Yucca faxoniana*. Expected but less frequently seen species include *Fraxinus greggii, Garrya ovata, Ptelea trifoliolata,* and *Muhlenbergia parviglumis*. Oaks and other more mesic species occur also at the highest summits and in more protected parts of drainages, even in steep drainages and lower elevations of the western slopes. These micro-niche species include *Malacomeles denticulata, Quercus pungens, Fendlera falcata, Fraxinus greggii, Prunus havardii,* and *Cheilanthes* spp.

Junipers, including *Juniperus coahuilensis* and *Juniperus pinchotii*, occur sporadically on the high plateaus amongst the chaparral clumps and, very rarely, in large, lower-elevation canyons. Pinyon pines are rare, documented only at a few eastern-slope locations. These species are probably relicts from the previously extensive juniper-pinyon-oak woodland covering the region between 22,000 and 11,000 years ago. The main pine of the DH is *Pinus remota*, a limestone specialist (Powell 1998). Once more widespread, *Pinus remota* in the Trans-Pecos is limited to isolated pockets, being more abundant on the Edwards Plateau and in Mexico. Records of *Pinus cembroides* in the DH are unusual; it is a higher-elevation taxon, although the two species are known to occur together elsewhere in the Big Bend region (Powell 1998).

Unique Habitats.—Several unique habitats were encountered during the course of the study; only the sand dunes at the mouth of Boquillas Canyon have been explored rather thoroughly. Though not extensive enough to support a full representation of Henrickson and Johnston's (1986) Sand Dune Scrub vegetation type, they have been well botanized and do provide a unique habitat for a few species including the rare *Chamaesyce golondrina* and the sand-loving species *Heliotropium convolvulaceum, Corispermum americanum,* and *Dalea terminalis*. Several other unusual vegetative areas would no doubt profit from further examination.

An isolated bottomland of *Pleuraphis mutica* covers the western edge of Ernst Basin, in stark contrast to the sparsely vegetated, more elevated flats over the rest of the basin. This tobosa grassland area may represent a small inclusion of Tornillo soils, which was previously unknown in the DH and is interesting not only because *Pleuraphis mutica* occurs in distinctly limited areas of BBNP, but because several other species were collected only there: *Malvella leprosa, Leptochloa panicea, Chamaesyce serpens,* and the Texas endemic *Lycium puberulum* var. *berberioides*. The possibility of similar habitats, i.e., the existence of Tornillo soils, in other large basins in the DH should be explored, in particular at the northern end of the Ore Terminal trail, in Margaret Basin, and along the Strawhouse trail.

The vegetation in a high saddle (5300 ft, 1615 m) just north and west of Sue Peaks was completely different from the immediate, Rosetófilo-type surrounding community. The soil was finer, deeper, and less

rocky than the surroundings; old wire, pieces of wood, and prehistoric lithic scatter including point bases and partial tools was found on the ground surface. Many plant species found there are reminiscent of the tobosa grassland area north of the Rosillos Mountains in the Harte Ranch area of BBNP, *Pleuraphis mutica*, *Panicum obtusum*, and *Hoffmannseggia drepanocarpa* in particular. Other species making up the unique community included *Sporobolus airoides*, *Sporobolus cryptandrus*, *Aristida adscensionis*, and *Muhlenbergia arenicola*.

The other habitats deserving of more attention are at the highest elevations, especially Sue Peaks and Stuarts Peak. Each has different characteristics making them interesting. Stuarts Peak is a rather narrow ridge, with not much area forming the actual summit. However, many plants collected there were surprising to find in such a seemingly arid location, including *Achnatherum curvifolium* and *Philadelphus microphyllus*. The lichen and moss flora on the summit ridge was impressive in its diversity, which was not observed to the same extent anywhere else in the study area. Also notable was that the summit ridge was one of the few places encountered where the cactus *Neolloydia conoidea* was growing densely enough as to preclude non-damaging travel.

The Sue Peaks area exhibits a well developed CHP community with shrub oaks being very common in the whole DH plateau area. The peaks themselves are rather bare of large shrubs, those being relegated to niches between boulders and ledges. Several species, found only in this area, were observed and collected on a trip following significant rains in the area: *Phemeranthus brevicaulis*, *Ipomoea costellata*, *Nama dichotomum*, *Dichromanthus cinnabarinus*, and *Mirabilis linearis*. These species, in addition to others known only from the peaks or the surrounding area including *Asplenium resiliens*, *Asclepias sperryi*, *Quercus mohriana*, *Fraxinus cuspidata*, *Quercus laceyi*, and *Pinus remota*, indicate that conditions on the whole are relatively mesic and that under favorable conditions, additional unique species may be in evidence.

Non-natives, Range Extensions, Rare Taxa, Notable Collections

Non-native species constitute a small part of the DH flora. The USDA considers 24 species collected in the DH as exotic (USDA 2007). Six of those species are considered invasive, and three are state-listed noxious weeds: *Arundo donax*, *Tamarix aphylla*, and *Tamarix chinensis* (PTI 2006). Significantly, *Pennisetum ciliare*, an introduced grass from Africa, is not among the Texas-listed invasives; however, it is a demonstrated threat to native ecosystems throughout the southwest (e.g., TNC 2005) and is listed by the state of Arizona as a noxious weed (AZDA 2005). The fact that it is widely planted in Texas and northern Mexico as a range grass perhaps makes its listing unlikely. *Eragrostis lehmanniana* is a well-known invasive in the desert southwest, but its presence in the study area appeared to be minimal outside of the river corridor. It seems to require more moisture than is reliably present in the majority of the range, with isolated plants being found near an old header dam and in shady or sandy areas of large drainages. Overall, non-native species constitute 3.6% of the DH flora.

Eleven species found in the DH are endemic to Texas, according to the Texas A&M Bioinformatics Working Group and updated taxonomic and distribution information (TAM-BWG 2006). The occurrence of *Matelea sagittifolia* in Brewster County is not currently reflected on the referenced website, but it was collected during the present study and also during a recent survey of the Lone Mountain area of BBNP (Fenstermacher et al. 2006). *Lycium puberulum* var. *berberioides* is also not listed by the Bioinformatics Working Group as occurring in the county but should be; it has been a known member of the BBNP flora for some time (Powell 1998). *Hedyotis pooleana*, though included in this DH-endemics list, is another species not listed by the Bioinformatics Working Group, perhaps due to the lack of consensus over its taxonomy (Turner 1995, 1997; Terrell 1996, 2001). Endemic species account for 1.7% of the DH flora.

Many noteworthy collections were made during the study period. The Wildlife Diversity Program of TPWD, in conjunction with the Texas Conservation Data Center of the Nature Conservancy of Texas, tracks seventeen rare species that were collected in the DH (TPWD 2006). Several of these species were collected at new locations. *Bouteloua kayi* was previously known only from one location east of the DH but it was found to be one of the dominant grasses at higher elevations near Sue Peaks. In the mid 1980s, *Hedyotis pooleana* was first collected at one locality in the DH and named as a new species. Subsequently it was not seen until the

present study during which it was found throughout the majority of the range in higher-elevation bedrock exposures.

Andrachne arida was last collected in the DH in the 1960s, and during the study period it was relocated in the general vicinity of the historical collections. One small population of the diminutive legume *Senna ripleyana* was discovered, clarifying its status as having remained extant north of the international border since its last documented collection in northern Brewster County in the 1940s. Another historically collected taxon *Sedum nanifolium* was encountered in shallow soil pockets on the DH plateau. Regionally it was previously known from one collection in the limestone mountains of northern Brewster County (Warnock 1977) and has been recently observed on hilltops of the Cox and Guadalupe ranches, about 15 mi (24 km) west of Sanderson (M. Terry pers. observ.).

One taxon, a member of the genus *Galactia*, as yet is not identified to the specific level. It does not fit descriptions of known Texan taxa (B. Turner pers. comm.) and awaits review when appropriate herbarium specimens become available. Populations have been found in several southern DH locations and the plant was encountered more commonly near the Rio Grande within side drainages of Boquillas Canyon. It is a sprawling, procumbent perennial from a central taproot, often growing vine-like within larger, surrounding vegetation. It has dense, silvery pubescence on all vegetative parts but is more pronounced on the leaves, those having prominent under-surface veins. The flowers are pink, the banner exhibits a green-yellow base, and the petals turn a deep blue-purple upon dessication.

New to the United States, the Mexican taxon *Seymeria falcata* var. *falcata* was collected north of the border originally in 1994 (*MT 137* SRSC), but it was not recognized as such until collections for the current study spurred a review of previous collections of its more widespread relative *Seymeria scabra* (Fenstermacher 2006).

Eight species were newly recorded for Brewster County, according to Turner et al. (2003) and known herbarium specimens: *Achnatherum curvifolium, Atriplex rosea, Argemone mexicana, Hedeoma serpyllifolia, Matelea sagittifolia, Maurandya wislizeni, Nama dichotomum,* and *Rumex maritimus*. Three of these species, *Atriplex rosea, Argemone mexicana,* and *Maurandya wislizeni*, were collected by NPS staff in conjunction with the restoration site at the mouth of Boquillas Canyon.

Many of the newly collected species for the DH are taxa that normally occur in much less arid conditions at the highest elevations in the Trans-Pecos. *Achnatherum curvifolium* is a C3 grass previously known from a restricted range in the Guadalupe Mountains of Texas and New Mexico (Powell 2000), and the nearby Delaware Mountains (*Worthington 24663* SRSC). *Nama dichotomum* is another elevation-restricted species, previously known from the Franklin, Davis, and Guadalupe Mountains. Its distribution ranges from Colorado down through the Mexican highlands and into temperate South America (Correll and Johnston 1970; Turner et al. 2003). In addition to the sparsely occurring relict taxa of *Juniperus* and *Pinus*, several other species were found whose presence was not expected in such relatively arid conditions: *Philadelphus microphyllus*, and several other C3 grasses *Achnatherum eminens, Achnatherum lobatum, Hesperostipa neomexicana,* and *Melica montezumae*. The DH are virtually the only area in the park where the giant dagger, *Yucca faxoniana*, occurs.

Interesting observations were made of dog cholla (*Opuntia* spp.) populations from the southern end of the study area. Dog cholla species of the southern Big Bend, most as part of the *Opuntia schottii* complex, have been of taxonomic interest for some time (Anthony 1956). The most recent attention in the literature documented that a long-believed hybrid, purportedly a cross between the tetraploids *Opuntia grahamii* and *O. schottii*, was finally determined to be a distinct species, *Opuntia aggeria*, based on morphology and its diploid nature (Ralston 1987, Ralston and Hilsenbeck 1989). During the current study, however, several observations and collections provide impetus for a fresh look a the taxonomy of southern Big Bend dog chollas: (1) a triploid hybrid was documented in the Ernst Tinaja area (*JF 635* SRSU; parents undetermined); (2) Diploid individuals with widely varying morphologies (e.g., *Fenstermacher 640, 1574* SRSC) may indicate that *Opuntia aggeria* has an even broader species concept than previously described by Ralston and Hilsenbeck (1989); (3) a tetraploid cholla was documented at Ernst Tinaja (*Fenstermacher 691* BIBE) with morphology

dissimilar to both *Opuntia schottii* and *O. grahamii*, possibly suggesting a larger distribution of *Opuntia densispina* in the Big Bend than previously surmised (Ralston and Hilsenbeck 1992, Powell and Weedin 2004); (4) all collections and individuals examined of *Opuntia grahamii* were sterile, effectively producing no pollen (J. Fenstermacher unpub. data). These findings suggest that the taxonomy of the *Opuntia schottii* complex is not completely understood; more data from Mexican populations may allow further resolution of the problem.

Floristic Analysis and Phytogeographic Connections

As a portion of Big Bend National Park, the flora of the DH is 54% of the park's listed total (NPS 1996) yet is found only on 24% of the land area. Clearly, this eastern side of the national park with its riverine and high-elevation habitats is an important source of area diversity. Comparisons with regional floras are hampered by their mostly out-of-date checklists, but exploring relationships to peripheral floristic areas and the larger southwest region is possible. One of clearest results of analyzing the DH flora is that while the Asteraceae is the most dominant family of the Southwestern flora (McLaughlin 1986), the Poaceae is co-dominant with Asteraceae in the DH and other southern Big Bend floras (Fenstermacher 2007). This suggests the connection to the Great Plains grasslands, moving into Texas through the High and Rolling Plains vegetation zones of the Panhandle region. The connection has also been quantitatively demonstrated by Christie (2006).

The Fabaceae is also important in the Southwest, but more important locally in the DH. This family comprises a larger percentage of the species of the SW flora than in the DH, yet the DH have more fabaceous species (52) than the average for SW floras (28). In fact, only five DH genera make the Southwestern flora's top-twenty list, and they do not include *Dalea*, one of the two dominant genera of the DH. The local importance of the Fabaceae, in addition to the many other resident thornscrub species like *Aloysia gratissima*, *Ziziphus obtusifolia*, and *Leucophyllum* spp., may indicate the importance of the Tamaulipan Thornscrub flora (WWF 2001). Indeed, for the few Trans-Pecos individuals of the more Tamaulipan species, *Acacia berlandieri*, *Croton torreyi*, and *Karwinskia humboltiana*, the Rio Grande corridor has most likely provided a conduit of limited habitat that enabled these species to extend their distributions upriver into generally more arid surroundings.

These connections to peripheral vegetational areas suggest that the CDR, and by extension the DH, are not simple extensions of the Sonoran region, as Cronquist suggests (1982). Rzedowski (1973) notes that both desert areas have several endemic genera (21 Sonoran, 16 CDR), which could suggest a long period of isolation and autochthonous development. In the same paper, comparisons of similarity index analyses show that the CDR flora has more affinity to the southern end of the Sierra Madre Oriental than it does to the Baja/Sonoran flora. Perhaps because there do not seem to be distinctive topographic limits to northern vegetative expansion, the limits of the CDR may be more climatically controlled (McLaughlin 1989): CDR flora shows more similarity to coastal Peru than to the Great Basin (Rzedowski 1973). Climate as a limiting factor becomes more significant when realizing that the Great Basin, Sonoran, and Chihuahuan deserts are linked topographically and geologically as members of the Basin and Range province.

Individual species' tolerances are probably what drove the paleovegetational changes in response to the changing climate. However, as McLaughlin (1986) points out, that is no reason why, on a larger scale, there cannot be found coherent assemblages of species occurring in non-random patterns. Many floristic regions, delineated as places where the climate acts upon the vegetation (as opposed to more local vegetational areas, using delimiters like soils or geography), have been applied to the Southwest (Dice 1943; Cronquist 1982; Takhtajan 1986; McLaughlin 1986; Bailey 1998). The boundaries of these large-scale, ecological regions can be drawn strictly using climate and gross vegetational features (Bailey 1998), by using centers of endemism to create distinct groupings (Cronquist 1982; Takhtajan 1986), which could be called a "scarceness" model, or the focus could be on the degree of overlap between individual floras throughout a region (McLaughlin 1986, 1989). This latter model does not focus on the dominant or rare taxa; rather, it takes into account all extant species and is a method based on "commonness." To this end, McLaughlin's (1986, 1989) work has provided floristically-based evidence supporting many historical floristic distinctions, intuitive or otherwise.

Interestingly, the area of southeast Arizona and southwest New Mexico, where Henrickson and John-

ston (2004) draw an arbitrary border of the CDR because of its perceived transitional nature, is shown by McLaughlin (1989) to be part of a distinct floristic area originally intuitively recognized by Dice (1943). McLaughlin's (1989) similarity indices identified an outlying connection between his so-called "Apachian" flora and the Davis Mountains region of the Big Bend, which Turner (1959) actually suggested in his floristic interpretation of the area. Also in support of this connection, the Davis Mountains, based on a subset of its flora (Larke 1989), has a family profile more similar to that of the Southwest (McLaughlin 1989), and is located more closely to the core of the Apachian element than to floras in the southern Big Bend.

The Apachian floristic element is thought to be autochthonous but allied to the Sierra Madre Occidental (McLaughlin 1989). Perhaps during the expansions and contractions of vegetation communities in response to Pleistocene climate change, this Apachian center extended its influence into the Big Bend. As many as 25 glacial-interglacial periods have affected the southwest (Henrickson & Johnston 2004), allowing more temperate plant species to expand into the Big Bend region from both the north and the south. In the Chisos Mountains of BBNP, *Pseudotsuga menziesii* and *Populus tremuloides* occur with the Mexican montane species *Cupressus arizonica* and what is believed to be *Pinus arizonica* (Powell 1998). In the DH, cooler-climate species that may be remnants of glacial expansion include *Achnatherum curvifolium* from the north and the Mexican pinyons from the south. In warmer times, the desert scrub and more tropical species expanded from the south. These climate fluctuations could have allowed for speciation through isolation, but there would have been more opportunities for diversification in the southern CDR, away from more extreme climate changes coming from the continental interior (Van Devender 1986). Of course, any discussion of speciation must acknowledge that the process is not simply a function of time or climate. Life forms, breeding systems, and genetics are also critical in producing differential speciation abilities (Grant 1958). However, perhaps more influential than genetic isolation, extinction may have been a more effective mechanism than speciation in affecting today's floristic diversity in the Big Bend.

More floristic study is warranted for the region. Beyond simply improving baseline knowledge of the Trans-Pecos flora, previous floristic work (McLaughlin 1986, 1989) should be revisited and improved by updating the original data, since the size of several Trans-Pecos floras have increased by 40–50% since the 1980s (e.g., Warnock 1967 *in* McLaughlin 1986 and Worthington 2001). Regionally, similarity index studies similar to those by McLaughlin (1986, 1989, 2007) and especially Christie (2006) could be used to elucidate in more detail the floristic influences on the Big Bend region and might help to identify more concretely the distinctions among CDR provinces. In this context, the completion of the present Dead Horse Mountains flora constitutes a significant step towards a more complete understanding of West Texas and regional floristic relationships.

ANNOTATED CHECKLIST OF VASCULAR PLANT TAXA

Species are arranged by divisions following Raven et al. (2003): Lycophyta, Pteridophyta, Coniferophyta, Gnetophyta, and Anthophyta. The flowering plants are subdivided into the classes Monocotyledones and Eudicotyledones. Within these hierarchical groupings, taxa are listed alphabetically by family, genus, species, and infraspecific rank as appropriate. Beyond a basic reliance on the *Manual of Vascular Plants of Texas* (Correll & Johnston 1970), taxonomy and nomenclature were taken preferentially from several updated sources, including Powell (in prep.) and Powell et al. (in ms.) for non-woody vascular species and genera, the *Flora of North America* volumes for the Poaceae and Asteraceae (FNA 2003b, 2006, 2007), and Powell and Weedin (2004) for the Cactaceae.

Online databases were consulted for currency, authors, and synonomy (ITIS 2007; MBG 2007; USDA 2007). Turner et al. (2003) was the fundamental source for nomenclature and distributional data. Specimens found through the herbaria search were assumed to be correctly identified except those that according to Turner et al. (2003) would have been far outside of their normal range. These were requested on loan, examined, and included or excluded from the final flora based on the resulting determinations (Fenstermacher2007). Native status, com (USDA 2007). Locally used common names from regional literature were included if not utilized by the USDA.

Table 3. Index to workers (initials and collectors name) who have made collections in the study area.

ACK	A.C. Koelling	DM	D. Miller	JM	J. Masters	RE	R. Eckhardt
AD	A. Denyas	DS	D. Seigler	JMM	J.M. Miller	RH	R. Halfmann
AG	A. Grimes	DS2	D. Smith	JMP	J.M. Poole	RLH	R.L. Hartman
AL	A. Freeman/A. Leavitt	DSC	D.S. Correll	JS	J. Sirotnak	RLU	R.L. Ufkes
AL2	A. Lewis	ECM	E. Castro-Mendoza	JT	J. Todd	RN	R. Nichols
AMP	A.M. Powell	EGM	E.G. Marsh	KJC	K.J. Castro	RRI	R. Rose-Innes
AT	A. Traverse	EJL	E.J. Lott	LCH	L.C. Hinckley	RS	R. Studhalter
B	Blevins	EW	Eula Whitehouse	LEB	L.E. Brown	SJ	S. Jones
BA	B. Alex	GJG	G.J. Goodman	LF	L. Fowle	SMU	SMU-DMNH
BA2	B. Amos	GJ	G. Jones	LJT	L.J. Toolin	SAP	S.A. Powell
BAR	B.A. Ralston	GLB	G.L. Bradley	LS	L. Slauson	SS	S. Sikes
BCT	B.C. Tharp	GLW	G.L. Webster	MA	M. Anthony	TA	T. Anderson
BD	B. Dodson	HBC	H.B. Correll	MC	M. Cole	TE	T. Emerson
BDGL	B.D.G. Leopold	HBP	H.B. Parks	MCJ	M.C. Johnston	TJW	T.J. Watson
BGH	B.G. Hughes	HC	H. Croad	MD	M. Darrach	TK	Tony Klein
BHW	B.H. Warnock	HCC	H.C. Cutler	MLP	M.L. Powell	TM	T. Mollhagen
BLT	B.L. Turner	HCH	H.C. Hanson	MPG	M.P. Griffith	TR	T. Rogers
BM	B. Moon	HKB	H.K. Beuchner	MSY	M.S. Young	TRV	T.R. Van Devender
BPM	Billy Pat McKinney	HL	Hillary Loring	MT	M. Talbot	TXDOT	Tx Highway Dept.
BR	B. Rector	HTF	H.T. Fletcher	MT2	M. Turner	UTW	U.T. Waterfall
BRM	B.R. McKinney	IMJ	I.M. Johnston	MWB	M.W. Bierner	VB	V. Bailey
CA	C. Adkins	JAM	J.A. Moore	MY	M. Yuhas	VLC	V.L. Cory
CAB	C.A. Bane	JAS	J.A. Steyermark	OCW	O.C. Wallmo	WBM	W.B. McDougall
CMR	C.M. Rowell	JC	J. Clark	OES	O.E. Sperry	WEH	W.E. Hall
CN	C. Newman	JDA	J.D. Allen	PAS	P.A. Smith	WFB	W.F. Barr
DAL	D.A. Louie	JDB	J.D. Bacon	PC	P. Cruze	WFM	W.F. Mahler
DAZ	D.A. Zimmerman	JEA	J.E. Averett	PDW	P.D. Whitson	WGD	W.G. Degenhardt
DB	D. Baker	JF	J. Fenstermacher	PM	P. Manning	WH	W. Hodgson
DB2	D. Benham	JFW	J.F. Weedin	PM2	P. McNeal	WOD	Justice W.O. Douglas
DF	D. Flyr	JH	J. Hardy	PVW	P.V. Wells	WRC	W.R. Carr
DG	D. Giles	JJ	J. Jernigan	RAH	R.A. Hilsenbeck		
DHR	D.H. Riskind	JLB	J.L. Blassingame	RB	R. Baker		

Various symbols precede the species entries: * = non-native; ! = invasive non-native; !! = noxious non-native (PTI 2006); **Δ** = observed but not collected; § = previously collected, but not during the current study period; **+** = first voucher of a common or expected taxon; # = newly documented taxon for the DH; o = species is shown to occur in the study area in Turner et al. (2003) but no voucher was found during the herbarium search; • = species is not shown to occur in study area in Turner et al. (2003) but previous voucher was discovered during herbarium search; ♦ = new county record; <u>*species name*</u> = new park record; **bold type** = rare (TPWD 2007). An explanation of rankings for rare species can be found in Poole et al. (2007). Abundance categories were based on Palmer et al. (1995) and ranked as follows: abundant = dominant or co-dominant in one or more common habitats; common = easily seen or found in one or more common habitats but not dominant in any common habitat; occasional = widely scattered but not difficult to find; uncommon = difficult to find with few individuals or colonies but found in several locations; rare = very difficult to find and limited to one or very few locations or uncommon habitats. Any historical abundance observations taken from label data are placed within quotations. The terms used historically were not changed (e.g., from "infrequent" to "uncommon"), because the previous collector's frame of reference or personal distinctions of scale categories is unknown. Many species may have a "rare" abundance within the study area but are not tracked by TPWD or TNC as being imperiled state- or worldwide and, thus, are not listed in bold and do not have a G or S ranking.

Vegetation communities: DSC = Desert Scrub; DAR = Desert Arroyo; DCA = Desert Canyon; RIO = Rio Grande Riparian Corridor; SYG = Sotol-Yucca Grassland; CHP = Chaparral. Two vegetation communities listed

together (e.g., SYG/CHP) indicate that the species was found in an intermediate matrix of vegetation types. More detailed habitat/substrate information, specific collection localities, and other notes are included in the MS thesis manuscript (Fenstermacher 2007).

All collections made during the current study are housed at SRSC. Selected duplicates were sent to BIBE, TEX-LL, and BRIT. All collections in the annotated list are grouped by the responsible herbarium. One hundred and sixteen collectors have contributed to the flora of the DH; initials were used for the names taken from the databases and are listed alphabetically by the first letter (Table 3).

LYCOPODIOPHYTA

Selaginellaceae

Selaginella lepidophylla (Hook. & Grev.) Spring, Resurrection fern, common perennial, DSC, DCA, SYG, 2200–4200 ft; *BA2 5391, JLB 3973, MC 158* (SAT); *BHW 18407, 10760, BHW & MCJ 15988, JF 253, MT 99, 420* (SRSC); *BHW 10760, BHW & RRI 562, DSC & BHW 14980, RRI & BM 1316a* (TEX-LL).

§ *Selaginella pilifera* A. Braun, Resurrection plant, perennial; *JLB 3980* (SAT).

Selaginella wrightii Hieron., Wright spikemoss, occasional to common perennial, DSC, DCA, SYG, 3500–4000 ft; *WFM 43* (BGWMA); *JF 458, 912, BHW 10827 & 18409, BHW & MCJ 15985* (SRSC); *BHW 10827, DSC & BHW 14981* (TEX-LL).

PTERIDOPHYTA

Aspleniaceae

+o *Asplenium resiliens* Kunze, Blackstem spleenwort, rare perennial, SYG, CHP, 5680–5840 ft; *JF 1279, 1993* (SRSC).

Pteridaceae

Argyrochosma limitanea (Maxon) Windham ssp. *mexicana* (Maxon) Windham, Southwestern false cloakfern, uncommon perennial herb, DCA, SYG, CHP, 2120–5840 ft; *JF 270, 432, 529, 675, 1504, 2023, 2198; AMP & SAP 6142* (SRSC).

Argyrochosma microphylla (Mett. ex Kuhn) Windham, Small leaf false cloakfern, occasional perennial, DSC, SYG, CHP, 2780–5000 ft; *JLB 2957, BA2 5392* (SAT); *JF 183, 484, 527, 768, 1175, 1198, BHW 10822* (SRSC), *BHW 10822, BHW & LCH BG-143* (TEX-LL).

Astrolepis cochisensis (Goodding) Benham & Windham, Cochise scaly cloakfern, common perennial, DSC, DCA, SYG, CHP, 1800–5500 ft; *WFM 58, BHW & LCH s.n.* (BGWMA); *PVW s.n.* (KANU); *JF 305, 953, 1232, 1257, 1546, 2098a, JF & MD 462, AMP & SAP 6143a, 6160, MT 54, BHW 10829, BHW & LCH BG-131, BHW & MCJ 16861* (SRSC); *BHW 10829* (TEX-LL).

Astrolepis integerrima (Hook.) Benham & Windham, Hybrid cloakfern, common perennial, DSC, SYG, 1900–4320 ft; *BA2 5393, 5578, 5579, JLB 938, 2599, HC 1, 32, 34* (SAT); *JF 206a, 433, 487, 680, 952, 1054, 1138, 1489, 1496, 1547, 2043, AMP & SAP 6143b, 6161, TR 88, 464, MT 55, BHW & MCJ 16068;* (SRSC); *DSC & BHW 14982a* (TEX-LL).

Astrolepis sinuata (Lag. ex Sw.) Benham & Windham, Wavy scaly cloakfern, uncommon perennial, DAR, DCA, 3050–3560 ft; *WFM s.n.* (BGWMA); *JLB 939, SJ 6510* (SAT); *JF 535, 1125, 1156* (SRSC); *DSC & BHW 14982* (TEX-LL).

+ *Astrolepis windhamii* Benham, Windham cloakfern, uncommon perennial, DSC, SYG, 2200–4700 ft; *JF 1697, 1705, 1892, 2202* (SRSC).

Cheilanthes alabamensis (Buckl.) Kunze, Alabama lipfern, rare perennial, DCA, SYG, 4650 ft; *JF 2199, MT 229* (SRSC); *MT 229* (TEX-LL).

§ *Cheilanthes bonariensis* (Willd.) Proctor, Golden lipfern, perennial, 4650 ft; *BA2 5394* (SAT).

Cheilanthes eatonii Baker, Eaton lipfern, occasional perennial, DSC, SYG, 3700–4960 ft; *JF 767, 1201, 1501, MT 116, BHW 20629* (SRSC).

Cheilanthes feei T. Moore, Slender lipfern, occasional perennial, DCA, SYG, 3050–4900 ft; *JF 533, 758, 1127, 1200, 1500, 1708, 1919, BHW 10765, 20605* (SRSC); *BHW 10765* (TEX-LL).

Cheilanthes horridula Maxon, Rough lipfern, occasional perennial, DAR, DCA, RIO, 1850–3050 ft; *CMR 2602* (BGWMA); *BA2 5498, 5580, HC 36, 40* (SAT); *JF 670, 1059, 1141, 1611, 2046, TR 465, BHW 18412, 20607* (SRSC); *DSC & BHW 14977* (TEX-LL).

Cheilanthes villosa Davenp. ex Maxon, Villous lipfern, uncommon perennial, DCA, 3560–3800 ft; *JLB 2596, 3801* (SAT); *JF 533a, BHW 10757* (SRSC); *BHW 10757, DSC & BHW 14983* (TEX-LL).

§ *Notholaena aschenborniana* Klotzsch, Scaled cloakfern, rare perennial; *JLB 2597, 2956* (SAT).

§ *Notholaena greggii* (Mett. ex Kuhn) Maxon, Gregg cloak fern, uncommon perennial, DCA, 1800–4300 ft; *CMR 2600* (BGWMA); *JLB 2600* (SAT); *BHW 10841, BHW 20897, BHW & LCH 16061, BHW & MCJ 16859* (SRSC); *DSC & BHW 14978, DS 1096* (TEX-LL).

Notholaena nealleyi Seaton ex J.M. Coult., Nealley cloak fern, rare perennial, DSC, DCA, 3650 ft; *JLB 3806* (SAT); *JF 479* (SRSC).

Notholaena neglecta Maxon, Maxon cloak fern, rare perennial, DCA, 1850–3560 ft; *JF 603, 1088* (SRSC); *DSC 14984, DSC & BHW 14979* (TEX-LL).

Notholaena standleyi Maxon, Star cloak fern, occasional perennial, DSC, DAR, DCA, SYG, 2880–4360 ft; *JLB 2595, KJC 176, HC 35, ECM 251* (SAT); *JF 604, 867, 1126, 1007a, BHW 9157, BHW & LCH 15987* (SRSC); *DSC & BHW 14985, BHW 9157* (TEX-LL).

Pellaea atropurpurea (L.) Link, Purple cliffbrake, rare perennial, SYG, CHP, 3500–5680 ft; *JF 1285, 1299a, 2200, BHW & LCH BG-144* (SRSC).

Pellaea intermedia Mett. ex Kuhn, Intermediate cliffbrake, rare perennial, SYG, CHP, 2560–4900 ft; *JF 1199, 2201, MT 119* (SRSC). *BHW 559* (TEX-LL).

CONIFEROPHYTA

Cupressaceae

Juniperus coahuilensis (Martínez) Gaussen [*Juniperus erythrocarpa* Cory], Rose-fruited juniper, rare shrub-tree, CHP, 4600–5470 ft; *JF 1240* (BIBE); *JF 1037, 1219, 1240, MT 237* (SRSC); *BA2 5370* (SAT).

Juniperus pinchotii Sudw., Red-berry Juniper, uncommon shrub-tree, DCA, SYG, CHP; 3050–5680 ft; *PVW s.n.* (KANU); *JF 499, 1048, 1136, 1298, 1913, AMP & SAP 5135, BHW & LCH BG-157* (SRSC).

Pinaceae

§ *Pinus cembroides* Zucc., Mexican pinyon, rare tree, SYG, ca. 4200–5300 ft; *WFM 54* (BGWMA); *BA2 5229* (SAT); *BHW 313* (SRSC).

Pinus remota (Little) D.K. Bailey & Hawksw., Papershell pinyon, rare tree, SYG, 5200 ft; *JF 1249, 1310, MT 88, 258, AMP 5492* (SRSC).

GNETOPHYTA

Ephedraceae

§ *Ephedra antisyphilitica* Berland. ex C.A. Mey., Clapweed, uncommon to "frequent" shrub, DSC, 3520 ft; *CMR 17227* (BIBE); *BHW 490* (SRSC & TEX-LL).

Ephedra aspera Engelm. ex S. Watson [*Ephedra nevadensis* var. *aspera* (Engelm. ex S. Watson) L.D. Benson], Rough jointfir, common shrub, DSC, DAR, DCA, SYG, CHP, 1900–5250 ft; *OES 1366* (BIBE); *BA2 5710, ECM 72, CMR 17227* (SAT); *JF 349, 455, 474, 563, 578, 723, 745a, 806, 1003, 1237, 1438, 1485, 1665, 2052, JF & MD 583, OES 1365, 1743, BHW 1742* (SRSC).

Ephedra trifurca Torr. ex S. Watson, Longleaf jointfir, common shrub, DSC, DCA, 1800–3500 ft; *EGM 143, ACK 830* (BIBE); *HCC 1856* (NYBG); *CMR 14224, 17225* (SAT); *JF 1388, BHW 47059* (SRSC); *BHW & RRI 557a, 57b, 47059* (TEX-LL).

ANTHOPHYTA, Monocotyledones

Agavaceae

#Δ *Agave havardiana* Trel., Havard century plant, rare shrub/semi-succulent, SYG, 5840 ft; South end of southern Sue Peak.

Agave lechuguilla Torr., Lechuguilla, abundant shrub/semi-succulent, DSC, DCA, SYG, 1800–5840 ft; *BA2 5264, DB s.n.* (SAT); *JF 257, TR 78* (SRSC); *MSY s.n.* (TEX-LL).

Amaryllidaceae

Cooperia drummondii Herbert, Evening rainlily, uncommon perennial herb, DSC, SYG, CHP 3150–5840 ft; *BA2 5686* (SAT); *JF 1102, 1984* (SRSC).

Zephyranthes longifolia Hemsl., Copper zephyrlily, rare perennial herb, DSC, SYG, 3500–4840 ft; *JF 584, BHW 1080-178* (SRSC).

Bromeliaceae

Hechtia texensis S. Watson [*Hechtia scariosa* L.B. Sm], Texas false agave, occasional shrub/semi-succulent, rock, DSC, 1800–4300 ft; *DG 219* (BIBE); *BA2 5253, 5273, DG 219, MC s.n.* (SAT); *JF 328, 1002, 1004, OES 1323, BHW 13036, 14047, 20625, 21206* (SRSC); *AT 2242* (TEX-LL).

Commelinaceae

Commelina erecta L., Whitemouth dayflower, rare perennial herb, DAR, DSC, 2300–2400 ft; *BRM 3032* (BGWMA); *JF 1445, OCW 507* (SRSC).

§ *Tradescantia wrightii* Rose & Bush var. *glandulopubescens* B.L. Turner, Wright spiderwort, rare perennial herb, 3800 ft; *BHW 10775* (SRSC & TEX-LL).

Cyperaceae

Carex muriculata F.J. Herm. [*Carex schiedeana* Kunze], Schiede sedge, uncommon perennial, SYG, 3000–5250 ft; *BHW & LCH BG-136* (BGWMA); *JF 2193* (BIBE); *BA2 5219, 5305* (SAT); *JF 772, 1193, 1236, 2193, MT 69, BHW 10821, 10847, BHW & LCH BG-136* (SRSC); *JF 1236, BHW 10821* (TEX-LL).

§ *Cladium mariscus* (L.) Pohl ssp. *jamaicense* (Crantz) Kükenth, Jamaica swamp sawgrass, uncommon perennial, ca. 1800 ft; *BHW 13068* (SRSC).

+o *Cyperus elegans* L., Royal flatsedge, rare perennial, DAR, 2400 ft; *JF 1449* (SRSC).

§ *Cyperus laevigatus* L., Smooth flatsedge, "rare" perennial, DCA, 1800 ft; *BHW 772* (SRSC).

§ *Cyperus odoratus* L., Fragrant flatsedge, "infrequent" annual or perennial, RIO, 1800 ft; *CAB 31* (BIBE); *JS s.n., EGM 162m, BHW 13046, 21441* (SRSC); *BHW 327* (TEX-LL).

§ *Cyperus squarrosus* L., Bearded flatsedge, "rare to infrequent" annual, RIO, 1800 ft; *BHW 774* (SRSC & TEX-LL).

§ *Eleocharis geniculata* (L.) Roemer & J.A. Schultes [*Eleocharis caribaea* (Rottb.) S.F. Blake], Canada spikesedge, "infrequent" annual, RIO, 1800 ft; *BHW 13047* (BIBE & SRSC); *BHW 772b* (TEX-LL). Last collected in 1955.

§ *Eleocharis montevidensis* Kunth, Sand spikerush, "frequent" annual, RIO, 1800 ft; *HTF 288* (SRSC).

§ *Eleocharis palustris* (L.) Roemer & J.A. Schultes [*Eleocharis macrostachya* Britton], Common spikerush, "frequent" perennial, ca. 3000 ft; *BHW & MCJ 16673* (SRSC).

§ *Fuirena simplex* Vahl var. *aristulata* (Torr.) Kral, Western umbrella-sedge, uncommon perennial, RIO, 1800 ft; *BA2 4605* (SAT); *BHW 21444* (SRSC & TEX-LL).

§ *Schoenoplectus pungens* (Vahl) Palla [*Scirpus americanus* Pers. var. *longispicatus* Britton], Common threesquare, perennial, *OES 1350* (SRSC).

Juncaceae

§ *Juncus acuminatus* Michx., Tapertip rush, perennial, 1800 ft; *CMR 17236* (SAT).

§ *Juncus bufonius* L., Toad rush, rare annual, RIO, 1800 ft; *BHW C298* (SRSC & TEX-LL).

Liliaceae

Allium kunthii G. Don, Kunth onion, rare perennial herb, SYG, 4700–5500 ft; *JF 1514, 1983* (SRSC).

Dasylirion leiophyllum Engelm. ex Trel., Sotol, common shrub/semi-succulent, DSC, DAR, DCA, SYG, CHP, ca. 3000–5840 ft *WFM s.n., TR s.n.* (BGWMA); *OES 1321* (BIBE); *JF 860, OES s.n.* (SRSC).

Nolina erumpens (Torr.) S. Watson, Foothill beargrass, shrub/semi-succulent, SYG, CHP, 4320 ft; *BA2 5704* (SAT); *JF 128, 821, AMP & SAP 5127, TR 130, MT 188, 190* (SRSC); *BHW & LCH BG-167* (SRSC & TEX-LL).

§ *Nolina texana* S. Watson, Texas sacahuista, rare shrub/semi-succulent; 3500 ft; *BHW & LCH s.n.* (BGWMA).

Nothoscordum bivalve (L.) Britt., Crowpoison, rare perennial herb; SYG; *BHW 10773* (SRSC). Collected in 1952 at the head of Heath Canyon.

§ *Yucca elata* Engelm., Soaptree yucca, shrub/semi-succulent, DSC, DCA, 3520 ft; *BA2 & DG 4861, BHW 877* (BIBE); *BA2 4861* (SAT); *BHW 877* (SRSC); *BHW 877, s.n., MSY s.n.* (TEX-LL).

§ *Yucca faxoniana* Sarg., Giant dagger yucca, occasional shrub/semi-succulent, DSC, SYG, CHP, 3500–5840 ft *OES 1322* (BIBE); *BRM s.n.* (BGWMA); *SMU 162* (SAT); *WH, TA, LS, & JP 9024, OWS 1322, MT 124* (SRSC); *RN E-4-6-92, 5-8-92, BHW Lot 45* (SRSC & TEX-LL).

Yucca rostrata Engelm. ex Trel., Beaked yucca, occasional shrub/semi-succulent, DSC, 2150–3400 ft; *PVW s.n.* (KANU); *WH, TA, LS & JP 9025, JF 849, TR 129, MT 50, BHW & LCH BG-62* (SRSC); *RN E-5-08-92, 4-6-1992* (TEX-LL).

§ *Yucca thompsoniana* Trel., Thompson yucca, occasional shrub/semi-succulent; *MSY s.n.* (TEX-LL).

Yucca torreyi Shafer, Torrey yucca, occasional shrub/semi-succulent, DSC, DAR, DCA, SYG, 2100–3500 ft; *SMU 164* (SAT); *WH, TA, LS & JP 9026, JF 683, 1723* (SRSC); *BHW 9940* (TEX-LL).

Orchidaceae

Dichromanthus cinnabarinus (Llave & Lex.) Garay, Scarlet ladies' tresses, rare perennial herb, SYG, 5500 ft; *JF 1958* (SRSC).

Poaceae

♦# *Achnatherum curvifolium* (Swallen) Barkworth [*Stipa curvifolia* Swallen], Guadalupe ricegrass, rare perennial herb, SYG, 5000 ft; *JF 735a* (SRSC).

Achnatherum eminens (Cav.) Barkworth [*Stipa eminens* Cav.], Southwestern needlegrass, rare perennial herb, DSC, SYG, 3400–5300 ft; *JF 366, 1990; BHW 10768* (SRSC); *BHW 10768* (TEX-LL).

Achnatherum lobatum (Swallen) Barkworth [*Stipa lobata* Swallen], Littleawn needlegrass, uncommon perennial herb, DSC, SYG, 3800–5000 ft; *JF 760, MT 146, BHW 10771* (SRSC); *BHW 10771* (TEX-LL).

§ *Andropogon glomeratus* (Walt.) B.S.P., Bushy bluestem, perennial herb, RIO, 1800 ft; *CAB 30* (BIBE).

+o *Aristida adscensionis* L., Six-weeks threeawn, rare annual herb, SYG, 5300–5840 ft; *JF 1304, 1918, 1987* (SRSC).

Aristida purpurea Nutt. var. *purpurea* [*Aristida roemeriana* Scheele], Purple threeawn, occasional perennial herb, DSC, DAR, DCA, 1800–3400 ft; *JF 173, 325, 344, 1327, 1382, 2079; MT 71* (SRSC).

Aristida purpurea Nutt. var. *nealleyi* (Vasey) Allred [*Aristida glauca* (Nees) Walp.], Blue threeawn, common perennial herb, DSC, DAR, DCA, SYG, 2250–4800 ft; *JF 486, 811, 935, 1178, 1192, 1536, 1537, CMR 5069, MT 70, 160, BHW 10758, 10811, 10816, 10835, BHW & LCH BG-159, 191, 193* (SRSC); *GJG & UTW 4628, BHW 10758, 10811, 10816, 10835, 13028* (TEX-LL).

§ *Aristida purpurea* Nutt. var. *wrightii* (Nash) Allred, Wright threeawn, perennial herb; 3500 ft; *BHW & LCH BG-159.*

§ *Aristida ternipes* Cav., Spidergrass, "frequent" perennial herb; 1800 ft; *BHW 20944, 20946; BHW & LCH BG-186* (SRSC).

!!+ *Arundo donax* L., Giant reed, abundant perennial herb, RIO, DCA, 1800 ft; *JF 2039* (SRSC).

+o *Blepharidachne bigelovii* (S. Wats.) Hack., Bigelow desertgrass, rare perennial herb, DSC, 3440 ft; *JF 355* (SRSC).

Bothriochloa barbinodis (Lag.) Herter, Cane bluestem, uncommon perennial herb, DAR, SYG, RIO, 1800–4400 ft; *BHW 779* (BIBE); *JF 1534* (SRSC).

Bothriochloa laguroides (DC.) Herter ssp. *torreyana* (Steud.) Allred & Gould, Silver Beardgrass, occasional perennial herb, DAR, DCA, 2350–4360 ft; *CMR 5096* (BGWMA); *JF 358, 531, 937, 1113, 1371, 1377, 1531, MT 198, 224, BHW s.n., BHW & BLT 8320* (SRSC); *BHW 21514, BHW & BLT 8320* (TEX-LL).

§ *Bouteloua aristidoides* (Kunth) Griseb., Needle grama, "frequent" annual herb, DSC, RIO, 1800 ft; *BA2, DG, TE, & PC 4597a, BHW 13034* (BIBE); *BHW 12894, 13034* (SRSC).

Bouteloua barbata Lag., Sixweeks grama, rare annual herb, RIO, DCA, 1800 ft; *BA2, DG, TE, & PC 4597b* (BIBE); *JF 2096* (SRSC).

Bouteloua curtipendula (Michx.) Torr. var. *caespitosa* Gould & Kapadia, Sideoats grama, common perennial herb, DSC, DAR, DCA, SYG, CHP, 1800–5250 ft; *JF 254, 1107, 1176, 1238, 1393, 1512, 1524, 2139, 2166, MT 38, 162, BHW 10780, BHW & LCH BG-190, BHW & BLT 8329* (SRSC); *BHW 10780* (TEX-LL).

+ *Bouteloua eriopoda* (Torr.) Torr., Black grama, rare perennial herb, SYG, 4400 ft; *JF 1533* (SRSC). Upper TC trail area.

+ *Bouteloua hirsuta* Lag., Hairy grama, occasional perennial herb, SYG, CHP, 3300–5500 ft; *JF 1221* (BIBE); *JF 1027, 1032, 1221, 1248, 1256, 1319, 1523, MT 46, 80, 131, 175* (SRSC).

Bouteloua kayi Warnock, Kay grama, uncommon (G1S1) perennial herb, DSC, SYG, CHP, 3500–5800 ft; *JF 2186* (BIBE, SRSC, & TEX-LL); *JF 296, 1169, MT 134, 182, 191, OCW 318, BHW 20621* (SRSC).

Bouteloua ramosa Scribn. ex Vasey, Chino grama, abundant perennial herb, DSC, DAR, DCA, SYG, CHP, 1800–4400 ft; *CMR 5075* (BGWMA); *JF 191, 338, 443, 930, 1160a, 1331, 1452, 1544, 1545, 2009, 2152, BHW 10853* (SRSC).

Bouteloua trifida Thurb., Red grama, occasional to "frequent" perennial herb, DSC, DAR, DCA, 1800–3360 ft; *JF 341, 1398, 1406, 1474, 1476, 1543, 2144, BHW 12341, 21190, BHW & LCH BG-183* (SRSC); *TRV, GLB & WEH 85-38* (TEX-LL).

Cathestecum erectum Vasey & Hack., False grama, occasional perennial herb, DSC, 1800–2450 ft; *JF 1340, MT 121, 141, BHW 10813, 12900, BHW & MCJ 16842* (SRSC); *BHW 110813, 12900* (TEX-LL).

§ *Cenchrus spinifex* Cav. [*Cenchrus incertus* M.A. Curtis], Coastal sandbur, locally frequent annual or perennial herb, RIO, DCA, 1800–2400 ft; *BA2, DG, TE, & PC 4601* (BIBE); *AMP & SAP 5862, BHW 23037, BHW & MCJ 16844, BHW & BLT 8322* (SRSC); *BHW 16844* (TEX-LL).

Chloris virgata Sw., Feather fingergrass, rare annual herb, DSC, RIO, 1800–3440 ft; *JF 364* (SRSC); *EGM 51-1129* (TEX-LL).

! *Cynodon dactylon* (L.) Pers., Bermudagrass, locally abundant perennial herb, DCA, RIO, 1800–2350 ft; *BA2, DG, TE, & PC 4610* (BIBE); *JF 1336* (SRSC); *EGM 141, 51-1115* (TEX-LL).

Dasyochloa pulchella (Kunth) Willd. ex Rydb. [*Erioneuron pulchellum* (Kunth) Tateoka; *Tridens pulchellus* (Kunth) Hitchc.], fluffgrass, occasional perennial herb, DSC, DCA, 1900–2760 ft; *BA2, DG, TE, & PC 4595* (BIBE); *JF 194, 678, 1338, 2025, 2049, BHW & LCH BG-198* (SRSC).

Digitaria californica (Benth.) Henr., Arizona cottontop, uncommon perennial herb, DSC, DAR, DCA, SYG, CHP, 3000–4000 ft; *CMR 5095* (BGWMA); *JF 335, 839, BHW 10801* (SRSC); *BHW 10801* (TEX-LL).

§ *Digitaria ciliaris* (Retz.) Koel., Southern crabgrass, rare annual herb, 1800 ft; *BHW 775* (BIBE, SRSC, TEX-LL).

+o *Digitaria pubiflora* (Vasey) J. Wipff [*Digitaria cognata*

(J.A. Schultes) Pilger var. *pubiflora* Vasey ex L.H. Dewey], Carolina crabgrass, rare perennial herb, DCA, 1800 ft; *JF 2121* (SRSC).

* *Echinochloa colona* (L.) Link, Junglerice, uncommon annual herb, DAR, RIO, 1800–3440 ft; *DG & TE 4611* (BIBE); *JF 1330, EGM 139, BHW 793* (SRSC); *EGM 51-1113, BHW 793* (TEX-LL).

§ *Echinochloa muricata* (Beauv.) Fern., Rough barnyardgrass, "rare" annual herb, RIO, 1800 ft; *BHW s.n.* (SRSC), *BHW C299* (TEX-LL).

Enneapogon desvauxii Desv. ex Beauv., Nineawn pappusgrass, occasional perennial herb, DAR, DCA, SYG, 1800–5000 ft; *JF 193, 231a, 347, 1510, 1551, 2097, BHW 10770, 12897, BHW & MCJ 16865* (SRSC); *BHW 10770* (TEX-LL).

Eragrostis intermedia A.S. Hitchc., Plains lovegrass, rare perennial herb, DSC, DCA, 2500–3800 ft; *JF 1894, BHW & MCJ 15984* (SRSC).

! *Eragrostis lehmanniana* Nees, Lehmann lovegrass, uncommon perennial herb, DAR, 2900–3440 ft; *CMR 16950* (BGWMA); *JF 211, 313, 1106, MT 202, BLT 22-143* (SRSC).

§ *Eragrostis pectinacea* (Michx.) Nees ex Steud., Tufted lovegrass, "infrequent" annual herb, RIO, 1800 ft; *BHW 785* (BIBE); *BHW C595* (TEX-LL).

Erioneuron avenaceum (Kunth) Tateoka, Shortleaf woolygrass, uncommon perennial herb, DSC, SYG, 3560–4400 ft; *JF 515, 1532* (SRSC); *BHW 10781* (TEX-LL).

Erioneuron pilosum (Buckl.) Nash, Hairy woolygrass, common perennial herb, DSC, DAR, DCA, SYG, CHP, 2150–5800 ft; *CMR 5089* (BGWMA); *JF 756, 850, 1031, 1057, 1179, 1225, 1251, 1271, 1992, 2160, JF & HL 1905, MT 44, 73, 174, 197, BHW 10781, BHW & LCH BG-75* (SRSC); *BHW 10789* (TEX-LL).

Hesperostipa neomexicana (Thurb. ex Coult.) Barkworth [*Stipa neomexicana* (Thurb. ex Coult.) Scribn], New mexico feathergrass, rare perennial herb, SYG, 5000 ft; *JF 735* (SRSC).

Heteropogon contortus (L.) Beauv. ex Roemer & J.A. Schultes, Tanglehead, occasional perennial herb, DAR, DCA, DSC, 1800–4400 ft; *JF 345, 574, 1396, 1473, 1596, 2138, MT 176, BHW 13074, 20947, BHW & LCH BG-189* (SRSC).

**Leptochloa dubia* (Kunth) Nees, Green sprangletop, uncommon perennial herb, DAR, SYG, 3750–5800 ft; *OCW 319* (BGWMA); *JF 233, 299, 1046, 1055, 1268, 1516, 1528, MT 231, OCW 319* (SRSC).

§ *Leptochloa fusca* (L.) Kunth ssp. *uninervia* (J. Presl) N. Snow [*Leptochloa uninervia* (J. Presl) A.S. Hitchc. & Chase], Mexican sprangletop, "infrequent to frequent" annual or perennial herb; RIO, 1800 ft; *HTF 289, BHW 13041* (SRSC); *EGM 140, 51-1114* (TEX-LL).

Leptochloa panicea (Retz.) Ohwi ssp. *mucronata* (Michx.) Nowack [*Leptochloa mucronata* (Michx.) Kunth], Mucronate sprangletop, rare annual or perennial herb, DSC, 2400 ft; *JF 1428* (SRSC).

Lycurus phleoides Kunth, Wolfstail, uncommon perennial herb, SYG, CHP, 3800–5000 ft; *JF 1034, MT 39, BHW 10769* (SRSC); *BHW 10769* (TEX-LL).

+o *Lycurus setosus* (Nutt.) C.G. Reeder, Bristly wolfstail, rare perennial herb, SYG, CHP, 5150 ft; *JF 1230* (SRSC). DH plateau.

+ *Melica montezumae* Piper, Montezuma melicgrass, rare perennial herb, DSC/DCA, 4040 ft; *JF 721* (SRSC).

Muhlenbergia arenicola Buckl., Sand muhly, rare perennial herb, SYG, 5300 ft; *JF 1253* (BIBE); *JF 1253, 1991* (SRSC).

Muhlenbergia dubia Fourn. ex Hemsl., Pine muhly, occasional perennial herb, DAR, SYG, 3500–5500 ft; *JF 734, 762, 1217, 1261, 2180* (SRSC). Possibly the dominant grass above 5000 ft.

Muhlenbergia porteri Scribn. ex Beal, Bush muhly, uncommon perennial herb, DSC, DAR, 2900 ft; *CMR 16956* (BGWMA); *JF 207* (SRSC).

+ *Muhlenbergia rigens* (Benth.) A.S. Hitchc., Deergrass, rare perennial herb, DAR/SYG, 4320 ft; *JF 1527* (SRSC).

§ *Muhlenbergia setifolia* Vasey, Curlyleaf muhly, perennial herb, DCA; *OCW 316* (BGWMA & SRSC).

Muhlenbergia spiciformis Trin. [*Muhlenbergia parviglumis* Vasey], Longawn muhly, occasional perennial herb, SYG, CHP, 4280–5840 ft; *JF 1053, 1216, 1243, 1262, 1303, 1513, 1525* (SRSC).

Muhlenbergia tenuifolia (Kunth) Trin., [*Muhlenbergia monticola* Buckl, Slender muhly, locally common annual or perennial herb, DCA, SYG, CHP, 5000 ft; *OCW 315b* (BGWMA & SRSC); *JF 845, 1191, 1489a, 1515, 1526, 1930, BHW 10750* (SRSC).

Panicum hallii Vasey, Hall panicgrass, common perennial herb, DSC, DAR, DCA, SYG, CHP, 2400–5150 ft; *CMR 5091* (BGWMA); *BHW 12893* (BIBE); *JF 195, 575, 1221a, 1229, 1395, 1456, 1519, 1921, MT 81, 211, BHW & LCH BG-192* (SRSC).

§ *Panicum hirticaule* J. Presl, Mexican panicgrass, uncommon annual herb, DSC, 1800–3800 ft; *BHW 12896* (BIBE); *BHW 10795* (SRSC & TEX-LL).

Panicum obtusum Kunth, Vine mesquite, rare perennial herb, SYG, 5300 ft; *JF 1997, TR s.n.* (SRSC).

Pappophorum bicolor Fourn., Pink pappusgrass, rare to "infrequent" perennial herb, DAR, DCA, 3050–3700 ft; *JF 1105* (BIBE & SRSC); *BHW 20629, BHW & LCH BG-166* (SRSC).

Pappophorum vaginatum Buckl., Whiplash pappusgrass, uncommon perennial herb, DSC, DAR, 2350–3480 ft; *JF 1394a* (BIBE & SRSC); *JF 1095, 1368, 1412, BHW & LCH BG-151* (SRSC).

* *Pennisetum ciliare* (L.) Link, [*Cenchrus ciliaris* L.], Buffelgrass, overall rare, but locally abundant perennial herb, DSC, DAR, DCA, RIO, 1850–2500 ft; *BA2 4323* (BIBE); *JF 1065, 2222; AMP 5861* (SRSC).

§ *Phragmites australis* (Cav.) Trin. ex Steud., Common reed, locally abundant perennial herb, RIO, 1800 ft; *WFM s.n.* (BIBE).

Pleuraphis mutica Buckl. [*Hilaria mutica* (Buckl.) Benth.], Tobosa grass, uncommon perennial herb, DSC, DAR, SYG, 2350–5300 ft; *DG & TE 4614* (BIBE); *JF 1255, 1399, 1435, 1478* (SRSC).

Poa bigelovii Vasey & Scribn., Bigelow bluegrass, uncommon annual herb, DSC, DCA, 3560 ft; *JF 516, 537, BHW 21134, 47056, BHW & MCJ 15982, 15984* (SRSC); *BHW 21134* (TEX-LL).

*§ *Polypogon monspeliensis* (L.) Desf. [*Alopecurus monspeliensis* L.], Rabbitfoot grass, locally occasional annual herb, RIO, 1800 ft; *HTF 290* (SRSC).

Schizachyrium scoparium (Michx.) Nash, Little bluestem, rare perennial herb, DCA, 3500–4650 ft; *JF 1950* (BIBE); *JF 1939, 1950, OCW 317* (SRSC).

+ *Setaria grisebachii* Fourn., Grisebach bristlegrass, rare annual herb, DSC, 2960 ft; *JF 217* (SRSC).

Setaria leucopila (Scribn. & Merr.) K. Schum., Streambed bristlegrass, occasional perennial herb, DSC, DAR, DCA, SYG, 2400–5300 ft; *JF 356, 1134, 1416, 1988, MT 102* (SRSC); *EGM 164* (TEX-LL).

§ *Setaria parviflora* (Poir.) Kerguélen [*Setaria geniculata* P. Beauv], Marsh bristlegrass, locally common perennial herb, RIO, 1800 ft; *CAB 32, BHW 13053* (BIBE); *BHW 13053* (SRSC); *EGM 51-1112, BHW 13053* (TEX-LL).

§ *Setaria reverchonii* (Vasey) Pilger, [*Setaria ramiseta* (Scribn.) Pilg.], Reverchon bristlegrass, perennial herb; 1800 ft; *BHW & MCJ 16856* (SRSC).

!+ *Sorghum halepense* (L.) Pers., Johnsongrass, rare perennial herb, DAR, 3440 ft; *JF 362* (SRSC).

Sporobolus airoides (Torr.) Torr., Alkali sacaton, uncommon perennial herb, DSC, SYG, 1800–5300 ft; *JF 1254, 1542, BGH 642* (SRSC).

Sporobolus cryptandrus (Torr.) Gray, Sand dropseed, uncommon perennial herb, DSC, DAR, DCA, SYG, 1800–5300 ft; *JF 352, 1999, 2050, 2146, MT 103* (SRSC).

§ *Sporobolus flexuosus* (Thurb. ex Vasey) Rydb., Mesa dropseed, "frequent" perennial herb, RIO, 1800 ft; *BHW & MCJ 16845, 16853* (SRSC).

§ *Sporobolus pyramidatus* (Lam.) A.S. Hitchc., Madagascar dropseed, "infrequent" annual or perennial herb, RIO, 1800 ft; *BHW 786* (SRSC).

§ *Sporobolus wrightii* Munro ex Scribn., Big sacaton, perennial herb; *EGM 123* (SRSC); *EGM 123, 51-1110* (TEX-LL).

§ *Tridens eragrostoides* (Vasey & Scribn.) Nash, Lovegrass tridens, perennial herb, 3700 ft; *BHW 20626* (SRSC).

Tridens muticus (Torr.) Nash, Slim tridens, common perennial herb, DSC, DAR, DCA, SYG, 1800–5500 ft; *JF 327* (BIBE); *JF 196, 208, 212, 327, 762a, 1017, 1039, 1174, 1177, 1260, 1369, 1437, 1475, 1937, 2017, 2078, TR 25, MT 138, 161, BHW 10789, 20628, BHW & LCH BG-65, BG-179* (SRSC).

Urochloa arizonica (Scribn. & Merr.) O. Morrone & F. Zuloaga [*Panicum arizonicum* Scribn. & Merr.], Arizona signalgrass, uncommon annual herb, RIO, DCA, 1800 ft; *JF 2105, BHW 12896, 20945, BHW & MCJ 16855* (SRSC).

§ *Vulpia octoflora* (Walt.) Rydb., Sixweeks fescue, annual herb, DCA; *RRI 21160* (TEX-LL).

Typhaceae

§ *Typha domingensis* Pers., Southern cattail, perennial herb, RIO, 1800 ft; *EGM 155* (SRSC); *BHW 835* (BIBE & TEX-LL).

ANTHOPHYTA, Eudicotyledones

Acanthaceae

Carlowrightia arizonica A. Gray, Arizona carlowrightia, uncommon subshrub, slickrock crevices, rocky soil, DSC, DAR, DCA, 1800–2350 ft; *BHW 12898* (BIBE); *JF 648, 1342, 2061, BHW 8334, 12898, 18408* (SRSC).

+ *Carlowrightia serpyllifolia* A. Gray, Trans-Pecos wrightwort, occasional subshrub, DSC, DCA, 3680 ft; *JF 447, 607, 667, 972, 1013, 1343, 2016, 2080* (SRSC).

● *Dyschoriste linearis* var. *cinerascens* (Henrickson & Hilsenb.) B.L. Turner, Polkadots, uncommon and "locally frequent" perennial herb, DSC, DAR, DCA, 2150–4360 ft; *BRM 3138, CMR 5093* (BGWMA); *BA2 5198, 5350, JF 1517, 1915, MT 65, BLT 22-145, BLT & BD 23-177, BHW & LCH 160* (SRSC); *BLT 22-145, BHW& LCH BG-87, BG-160* (TEX-LL).

● *Justicia pilosella* (Nees) Hilsenb., Gregg tubetounge, uncommon perennial herb, DSC, DAR, DCA, 2100–3050 ft; *JF 1133, 1351, TRV s.n., BHW 21195* (SRSC).

Justicia warnockii B.L. Turner, Warnock water-willow, occasional subshrub, DSC, DAR, DCA, 1800–3720 ft; *BHW & LCH BG-137* (BGWMA); *AL 161, 162, CMR 17231, BHW 13063(266)* (BIBE); *JF 229, 687, 1667, 2053, 2087, MT 152, 181, 227, BLT 22-149, BLT & BD 23-178, BHW 10786, 13063, 20410, BHW & LCH BG-137, BHW & MCJ 16827* (SRSC); *BLT 22-149, BLT & BD 23-178, BHW 10786, BHW & LCH s.n.* (TEX-LL).

Ruellia parryi A. Gray, Parry wild petunia, common subshrub, DSC, DAR, DCA, 1800–4600 ft; *SMU 48* (BGWMA); *JF 202, 434, 520, 829, 945, 2042, 2113, AMP & SAP 5136, MT 27, BLT 22-144* (SRSC); *BLT 22-144* (TEX-LL).

Amaranthaceae

*+ *Amaranthus blitoides* S. Wats., Mat amaranth, rare annual herb, DAR, 3000 ft; *JF 218* (SRSC).

§ *Amaranthus palmeri* S. Wats., Carelessweed, annual herb, RIO, 1800 ft; *EGM 125, 128, 136* (BIBE).

Amaranthus scleropoides Uline & Bray, Bonebract amaranth, rare annual herb, DCA, 1800 ft; *JF 2107* (SRSC).

§ *Amaranthus torreyi* (Gray) Benth. ex S. Wats., Torrey amaranthus, "frequent" annual herb, DSC, 3800 ft; *BHW 10796* (SRSC & TEX-LL).

§ *Froelichia arizonica* Thornb. ex Standl., Arizona snakecotton, "occasional" perennial herb, DSC, DAR, DCA; *BHW & BLT 8318, BHW & MCJ 16847, GLW 4477* (SRSC); *DSC & HBC 30635, BLT & MT2 97-333* (TEX-LL).

Tidestromia lanuginosa (Nutt.) Standl., Wooly tidestromia, uncommon annual herb, DSC, DCA, 2850 ft; *JF 942, BHW & MCJ 16852* (SRSC).

Tidestromia suffruticosa (Torr.) Standl., Shrubby honeysweet, occasional subshrub, DSC, DCA, 1800–2760 ft; *JF 149, 197, BHW 694* (SRSC); *BHW 694* (TEX-LL).

Anacardiaceae

Rhus microphylla Engelm. ex A. Gray, Littleleaf sumac, rare shrub, DAR, 2100–2400 ft; *CMR 5076* (BGWMA); *JF 1444, BHW & LCH BG-89* (SRSC).

Rhus trilobata var. *pilosissima* Engl., Skunkbush sumac, rare shrub, CHP, 5680 ft; *JF 1292* (SRSC).

Rhus virens Lindh. ex A. Gray var. *virens*, Evergreen sumac, uncommon to occasional shrub, DCA, CHP, 3050–5680 ft; *CMR 15830* (BGWMA); *JF 767a, 1040, 1135, 1182, 1295, 1508* (SRSC).

Apocynaceae

<u>*Haplophyton crooksii*</u> (L.D. Benson) L.D. Benson [*Haplophyton cimicidum* A. DC. var. *crooksii* L. Benson], Cockroach plant, rare perennial herb, DCA, 1850 ft; *JF 1067* (SRSC).

Telosiphonia macrosiphon (Torr.) Henrickson, [*Macrosiphonia macrosiphon* (Torr.) A. Heller], Rocktrumpet, uncommon subshrub, DSC, DAR, 2700–3350 ft; *CMR 11625* (BGWMA); *JF 815, 933, 1481* (SRSC).

Aristolochiaceae

Aristolochia coryi I.M. Johnst., Dutchman pipe, occasional perennial herb, DSC, DAR, DCA, RIO, SYG, 1800–4280 ft; *BA2, DG, TE, & B 4933* (BIBE); *BA2 5716* (SAT); *JF 955, 1483, 1491, 2093, 2119, BLT & MT2 97-338, BHW 8332* (SRSC); *BLT & MT2 97-338* (TEX-LL).

Asclepiadaceae

+ *Asclepias asperula* (Dcne.) Woods., Spider milkweed, uncommon perennial herb, DSC, 2560–3800 ft; *JF 368, 1405, 1911* (SRSC).

Asclepias oenotheroides Cham. & Schlecht., Zizotes milkweed, rare perennial herb, DSC, DCA, 2300–2750 ft; *JF 914* (SRSC); *BLT & MT2 97-341* (TEX-LL).

Asclepias sperryi Woods., Sperry milkweed, rare subshrub, CHP, 5100–5680 ft; *JF 1286, 2194* (SRSC).

§ *Cynanchum barbigerum* (Scheele) Shinners, Bearded swallow-wort, perennial herbaceous vine; *JLB 870* (SAT).

Cynanchum pringlei (Gray) Henrickson, [*Cynanchum barbigerum* var. *breviflorum* Shinners], Pringle swallow-wort, uncommon to occasional perennial herbaceous vine, DSC, DAR, DCA, 3000–4240 ft; *BA2 5315* (SAT); *JF 256, 301, 1164, 1488, 2203, MT 30, BLT & BD 23-174, BHW 10785, BHW & LCH BG-133* (SRSC); *BLT & BD 23-173, BHW 10785, BHW & LCH BG-133* (TEX-LL).

Cynanchum racemosum (Jacq.) Jacq. var. *unifarium* (Scheele) E. Sundell, [*Cynanchum unifarium* (Scheele) Woodson], Talayote, uncommon to locally common perennial herbaceous vine, DAR, DCA, 2780–4040 ft; *JF 1928, AL 144* (BIBE); *BA2 5317* (SAT); *JF 169, 858, 1928* (SRSC).

Matelea parvifolia (Torr.) Woods., Spearleaf milkvine, rare perennial herbaceous vine, DSC/DAR, 1900 ft; *JF 2057* (SRSC).

§ *Matelea producta* (Torr.) Woods., Texas milkvine, perennial herbaceous vine, RIO, 1800 ft; *BHW 13050* (BIBE).

Matelea reticulata (Engelm. ex Gray) Woods., Netted milkvine, uncommon perennial herbaceous vine, DAR, DCA, 3160–4600 ft; *BRM 3225, BHW & LCH BG-170* (BGWMA); *JF 1938* (BIBE); *BA2 5339* (SAT); *JF 221, 1938, JF & MY 1317, AMP & SAP 5132, BHW & LCH BG-170* (SRSC).

#♦ *Matelea sagittifolia* (Gray) Woods., Arrowleaf milkvine, rare perennial herbaceous vine, DSC, 3350 ft; *JF 1484* (SRSC).

§ *Sarcostemma crispum* Benth., Wavyleaf twinvine, perennial herbaceous vine, DSC; *TR 147* (BGWMA); *BA2 5365* (SAT).

§ *Sarcostemma cynanchoides* Dcne. var. *cynanchoides*, Fringed twinevine, "frequent on shrubs", perennial herbaceous vine, RIO, DSC, 1825 ft; *BA2 & DG 5158* (BIBE); *BHW 13050* (TEX-LL).

Sarcostemma cynanchoides Dcne. var. *hartwegii* (Vail) Shinners, Hartweg twinevine, rare perennial herbaceous vine, DSC, DCA, 1800–2350 ft; *JF 1347* (SRSC); *BHW 12904* (BIBE, SRSC, TEX-LL).

Sarcostemma torreyi (Gray) Woods., Soft twinevine, uncommon perennial herbaceous vine, DAR, DCA, RIO, 1800–4650 ft; *BA2 5223, 5280, 5375* (SAT); *JF 1956, 2000, TR 147, BHW 13050, BHW & LCH BG-165* (SRSC).

Asteraceae

Acourtia runcinata (Lag. ex D. Don) B.L. Turner, Featherleaf desertpeony, occasional perennial herb, DSC, DCA, 1800–3700 ft; *BRM 3147* (BGWMA); *BA2 5217, 5440* (SAT); *JF 147, 302, 459, 1339, 1353, 2115, OCW 342, BHW 10815, 20610, BHW & LCH BG-181, BHW & MCJ 15899* (SRSC); *BLT & MT 97-339, BHW 10815* (TEX-LL).

Ageratina wrightii (A. Gray) R.M. King & H. Rob., [*Eupatorium wrightii* A. Gray], Wright snakeroot, uncommon shrub, DSC, DCA, SYG, 4040–4900 ft; *OCW s.n.* (BGWMA); *JF 722, 1549, 2189; OCW 336* (SRSC); *BA2 5481, 5457* (TEX-LL).

§ *Ambrosia confertiflora* DC., Weakleaf burr ragweed, perennial herb; *BA2 5360* (SAT).

§ *Aphanostephus ramosissimus* DC. var. *humilis* (Benth.) B.L. Turner & Birdsong, Plains dozedaisy, annual herb, DCA, RIO, 1800–2560 ft; *AL 310* (BIBE); *VLC 18730* (TEX-LL).

Artemisia ludoviciana Nutt. var. *ludoviciana*, White sagebrush, occasional perennial herb, DSC, DAR, DCA, SYG, CHP, 3050–5680 ft; *BA2 5491* (SAT); *JF 222a, 1152* (SRSC); *BA2, DG & TE 5491* (TEX-LL).

Baccharis havardii Gray, Havard false willow, rare subshrub, DAR, DCA, 4050–4350 ft; *JF 1933, 1941* (SRSC).

Baccharis salicifolia (Ruiz & Pavón) Pers., [*Baccharis glutinosa* Pers.], Seepwillow, jara, locally common shrub, DAR, DCA, RIO, 1800–4280 ft; *EGM 12* (BIBE); *BA2 5511* (SAT); *JF 1345* (SRSC); *BA2, DG & ET 5511* (TEX-LL).

§● *Baccharis salicina* Torr. & Gray, Great plains false willow, subshrub, DSC; *BGH 643* (SRSC).

Bahia absinthifolia Benth. var. *dealbata* (Gray) Gray, Dealbata bahia, common perennial herb, DSC, DAR, 1800–3560 ft; *BHW 12888* (BIBE); *JF 347a, 543, 810, 2109, MT 120, 235, 253, BHW 12888, GLW 4486* (SRSC); *BA2 & TE 5301, BHW 12888* (TEX-LL).

Bahia pedata Gray, Bluntscale bahia, uncommon annual herb, DSC, DCA, 3050–3150 ft; *JF 1102a, 1104* (SRSC); *WFB 67* (TEX-LL).

Baileya multiradiata Harvey & Gray ex Gray, Desert marigold, common to occasional annual herb, DSC, DAR, DCA, 2400–3050 ft; *BA2, DG, TE, & PC 4598, CN 1194;* (BIBE); *JF 1132, 1455, 1466, MT 16* (SRSC).

Brickellia coulteri Gray, Coulter brickellia, occasional subshrub, wash gravel, crevices in bedrock, rocky soil, DSC, DAR, DCA, RIO, 1800–3800 ft; *JF 686, 1061, 1593, 1669, 2064; BHW 10834* (SRSC); *DSC & HBC 30626, BHW 10834* (TEX-LL).

Brickellia eupatorioides (L.) Shinners var. *chlorolepis* (Woot. & Standl.) B.L. Turner, False boneset, rare subshrub, DSC, DAR, 4280 ft; *BA2 5510* (SAT & TEX-LL); *JF 1041* (SRSC).

Brickellia laciniata Gray, Splitleaf brickellia, occasional shrub, DAR, DCA, 1850–3050 ft; *BA2 5483* (SAT & TEX-LL); *JF 1084, 1146* (SRSC).

● *Brickellia lemmonii* var. *conduplicata* (B.L. Rob.) B.L. Turner, Lemmon brickellbush, uncommon perennial herb, DCA, 4650 ft; *BA2 5441, DG 328, 329* (SAT); *JF 1944, 1949* (SRSC); *BA2 5455, BA2 & TE 5441* (TEX-LL).

+ *Chaetopappa bellioides* (Gray) Shinners, Manyflower leastdaisy, rare perennial herb, DSC, 2680 ft; *JF 190* (SRSC).

+ *Chaetopappa ericoides* (Torr.) Nesomn [*Leucelene ericoides* (Torr.) Greene], Rose heath, leucelene, rare annual or perennial herb, SYG, 5000–5300 ft; *JF 773, 2157* (SRSC).

Chloracantha spinosa (Benth.) Nesom, [*Aster spinosus* Benth., *Erigeron ortegae* S.F. Blake], Mexican devilweed, occasional

perennial herb, RIO, 1800 ft; *BA2, DG, TE, & B 4922* (BIBE); *JF 2019a* (SRSC).

Chrysactinia mexicana A. Gray, Damianita, common subshrub at higher elevations, DCA, SYG, CHP, 4080–5200 ft; *SMU 52* (BGWMA); *PVW s.n.* (KANU); *BA2 5297* (SAT); *JF 572, MT 223* (SRSC); *BA2 & TE 5297* (TEX-LL).

Cirsium turneri Warnock, Cliff thistle, uncommon perennial herb, DCA, 2920–4200 ft; *AL 163* (BIBE); *JF 187, 1121, 1704, AMP & SAP 5126, MT 215* (SRSC); *JF 1121* (TEX-LL).

§ *Conyza canadensis* (L.) Cronq., Canadian horseweed, annual herb; *EGM 142* (BIBE).

Diaperia verna (Raf.) Morefield, [*Evax verna* Raf.; *Evax multicaulis* DC.], Manystem evax, rare annual herb, DSC, DAR, 2400–2520 ft; *JF 1429* (SRSC); *RRI 555* (TEX-LL).

Dyssodia acerosa DC., [*Thymophylla acerosa* (DC.) Strother], Prickleleaf dogweed, common perennial herb, DSC, DAR, DCA, 2150–4400 ft; *BHW & LCH BG-72* (BGWMA); *JF 512, 1588, MT 72, BHW & LCH BG-72, GLW 4447* (SRSC); *BA2, DG & TE 5505* (TEX-LL).

Dyssodia micropoides (DC.) Loes., [*Thymophylla micropoides* (DC.) Strother], Wooly dogweed, uncommon perennial herb, DSC, 2350–2560 ft; *AL 316, 317* (BIBE); *JF 1401, 1684* (SRSC); *BA2, DG & TE 5461* (TEX-LL).

Dyssodia pentachaeta (DC.) B.L. Robins., [*Thymophylla pentachaeta* (DC.) Small var. *pentachaeta*], Prickly dogweed, occasional perennial herb, DSC, DAR, DCA, SYG, 1800–5150 ft; *CMR 5056* (BGWMA); *BA2, DG, TE, & PC 4599* (BIBE); *PVW s.n.* (KANU); *JF 192, 320, 460, 540c, 542, 576, 1033, 1085, 1226, 1228, 1927, 2108, HTF 1230, MT 62, 242, BHW 10817* (SRSC); *BA2 & TE 5295, 5296* (TEX-LL).

§ *Eclipta prostrata* (L.) L., [*Eclipta alba* (L.) Hassk.], False daisy, "infrequent to frequent" annual or perennial herb, RIO, 1800–1825 ft; *BHW 13039* (BIBE, SRSC, TEX-LL); *BHW 13035* (TEX-LL).

Erigeron flagellaris A. Gray, Trailing fleabane, uncommon biennial herb, 3300–4600 ft; *JF 754, 799, AMP & SAP 5129, MT 78* (SRSC).

Erigeron modestus Gray, Plains fleabane, uncommon perennial herb, DSC, DAR, 3460 ft; *VLC 43989; JF 264, 373, MT 249* (SRSC); *BA2 & TE 5324, BA2, TE & DG 5494* (TEX-LL).

Erigeron tracyi Greene, [*Erigeron colomexicanus* A. Nels.], Running fleabane, occasional annual herb, DSC, DAR, DCA, SYG, 2880–5150 ft; *JF 1025* (BIBE); *JF 763, 1008, 1025, 1153, 1231, 1272, BLT & BD 23-170, BHW 10833* (SRSC); *BLT & BD 23-170* (TEX-LL).

§ *Flaveria trinervia* (Spreng.) C. Mohr, Running yellowtops, "frequent" annual herb, RIO, 1800 ft; *EGM 132, BHW 750, 13042* (BIBE); *BHW 13042* (SRSC); *EGM 132, BHW 750* (TEX-LL).

§ *Flourensia cernua* DC., Tarbush, rare shrub; *BA2 5520* (TEX-LL).

§ *Flyriella parryi* (Gray) King & H.E. Robins., Chisos mountains brickellbush, "infrequent" perennial herb; *BHW 18403* (SRSC).

Grindelia arizonica Gray, Arizona gumweed, annual or perennial herb, SYG, 4280 ft; *JF 1043* (SRSC).

§● *Grindelia nuda* Wood var. *nuda*, Curlytop gumweed, annual or perennial herb, DAR; *BA2 & TE 5355* (TEX-LL).

Gutierrezia microcephala (DC.) Gray , Threadleaf snakeweed, occasional to locally common subshrub, DAR, DCA, DSC, SYG, 2500–5840 ft; *JF 1324a, MT 45, 219, 252* (SRSC); *BA2, DG, & TE 5521, TR 251* (TEX-LL).

Gutierrezia sarothrae (Pursh) Britt. & Rusby, Broom snakeweed, common subshrub, DSC, DAR, DCA, RIO, SYG, 1800–5100 ft; *BA2, DG, B & TE 4921, JF 1411* (BIBE); *PVW s.n.* (KANU); *JF 318, 1411, 1417, TR 251, BLT & BD 23-179* (SRSC).

Gutierrezia sphaerocephala Gray, Roundleaf snakeweed, uncommon subshrub, DSC, DAR, SYG, 2400–4280 ft; *JF 1411a, OES 763* (SRSC); *BLT & BD 23-179* (TEX-LL).

Gymnosperma glutinosum (Spreng.) Less., [*Xanthocephalum glutinosum* (Spreng.) Shinners], Tatalencho, gumhead, common subshrub, DSC, DAR, DCA, SYG, 2350–5300 ft; *OCW 339* (BGWMA); *JF 238, 321, 498a, 579, 712, 752, 1181, 1376, 1989, OCW 339* (SRSC); *BA2 & TE 5323, BA2, DG & TE 5515* (TEX-LL).

§ *Helenium elegans* DC. var. *amphilobum* (Gray) Bierner, Pretty sneezeweed, annual herb, RIO, 1800 ft; *MWB & JEA 232a, 232c, 232d* (TEX-LL).

§ *Helenium microcephalum* DC. var. *microcephalum*, Smallhead sneezeweed, "frequent" annual herb, RIO, 1800 ft; *AL 322, CN 504* (BIBE); *BHW 13031* (SRSC); *OES & CN 504, BHW 13031* (TEX-LL).

§ *Helenium microcephalum* DC. var. *ooclinium* (Gray) Bierner, [*Helenium ooclinium* A. Gray], annual herb, RIO, 1800 ft; *MWB & JEA 232b, 232e* (TEX-LL).

Helianthus annuus L., Common sunflower, "frequent" annual herb, RIO, 1800 ft; *EGM 129, BHW 13045* (BIBE); *JF 2263, BHW 13045* (SRSC).

§ *Helianthus ciliaris* DC., Texas blueweed, "locally frequent" perennial herb, RIO, 1800 ft; *BHW 13051* (BIBE & SRSC).

Heliopsis parvifolia Gray, Mountain oxeye, rare perennial herb, SYG/CHP, 5680 ft; *JF 1276* (BIBE & SRSC).

§ *Isocoma pluriflora* (Torr. & Gray) Greene, [*Haplopappus heterophyllus* (A. Gray) S.F. Blake; *Haplopappus pluriflorus* (Torr. & A. Gray) H.M. Hall], Jimmyweed, subshrub, DSC; *BHW 1076* (TEX-LL).

Iva ambrosiifolia (Gray) Gray, Rag sumpweed, ragged marshelder, rare annual herb, DSC, DAR, 3640 ft; *JF 289* (SRSC); *BA2, DG, & TE 5492* (TEX-LL).

Jefea brevifolia (A. Gray) Strother, [*Zexmenia brevifolia* A. Gray], Shorthorn zexmenia, occasional shrub, DSC, DCA, SYG, 1800–4700 ft; *PVW s.n.* (KANU); *JF 472, 708, 2132, CMR 5068, MT 106, BHW 10736* (SRSC); *BA2, DG, & TE 5503, BA2 & TE 5298, DF 223, BHW 10763* (TEX-LL).

+ *Laennecia coulteri* (Gray) Nesom, [*Conyza coulteri* A. Gray], Coulter horseweed, annual horsetail, rare annual herb, DCA, 2400 ft; *JF 1420* (SRSC).

+○ *Machaeranthera tanacetifolia* (Kunth) Nees, Tahoka daisy, rare annual herb; DAR, 3480 ft; *JF 544* (SRSC).

Melampodium leucanthum Torr. & A. Gray, Blackfoot daisy, occasional subshrub, DSC, DAR, DCA, RIO, SYG, 1800–4450 ft; *JF 228, 269, 490, 967, 2006, 2123, MT 4, 47, 58, 74, 238, BLT & BD 23-176, BHW & BLT 8328, GLW 4483* (SRSC); *BLT & BD 23-176* (TEX-LL).

+ *Packera millelobata* (Rydb.) W.A. Weber & A. Löve, Uinta ragwort, rare perennial herb, SYG/CHP, 5680–5840 ft; *JF 1287, 1971* (SRSC).

Parthenium argentatum A. Gray, Guayule, locally uncommon to occasional, DSC, SYG, 2920–4880 ft; *BHW & LCH BG-177* (BGWMA); *JF 1024, BDGL s.n.* (BIBE); *PVW s.n.* (KANU); *JF 744, 1024, 1139, 1155, 1183, 1901, JMM 888, 900, 903, AMP & SAP 4297, MT 49, BHW 10753* (SRSC); *BHW 10753* (TEX-LL).

Parthenium confertum A. Gray, Lyreleaf parthenium, uncommon to occasional annual or biennial herb, DSC, DAR, DCA, 1850–5840 ft; *JF 206, 359a, 524, 852, 1068, 1083, 1433, 1907, DM & JC 380, 900, 904, MT 41, 254, BHW 20608, BHW & MCJ 16836* (SRSC); *BA2 & TE 5304* (TEX-LL).

Parthenium incanum Kunth, Mariola, common shrub, DSC, DAR, DCA, SYG, 2300–5000 ft; *JF 350, 1023, OCW 511* (SRSC); *BA2 & TE 5303* (TEX-LL).

§ *Pectis angustifolia* Torr. var. *angustifolia*, Limoncillo, "frequent" annual herb; *BHW & BLT 8323* (SRSC); *VLC 30209, DF 224* (TEX-LL).

§ *Pectis papposa* Harvey & Gray var. *grandis* Keil, Manybristle cinchweed, "frequent in sandy soil" annual herb, 1800 ft; *BHW 286* (SRSC); *BHW & BLT 8323* (TEX-LL).

Perityle aglossa A. Gray, Bluff rockdaisy, occasional subshrub, cracks, DSC, DCA, 1850–3560 ft; *AL 141* (BIBE); *JF 184, 530, 650, 685, 1005, 1007, 1073, 1350, 2014, SS 38, 931, BHW 20409* (SRSC); *SS 931* (TEX-LL).

Perityle bisetosa (Torr. ex A. Gray) Shinners var. ***scalaris*** A.M. Powell, Stairstep rockdaisy, uncommon to occasional (G2T1S1) subshrub, DCA, SYG, CHP, 3050–5680 ft; *AL 146* (BIBE); *JF 475, 608a, 1123, 1289, 1917, BHW 20604* (SRSC); *JMP 2742* (TEX-LL).

Perityle vaseyi J.M. Coult., Vasey rockdaisy, rare subshrub, rocky soil; DSC, DAR, 2080–2350 ft; *JF 1367, SS 39, TRV & LJT 1816* (SRSC); *SS 39* (TEX-LL).

+ *Plectocephalus americanus* (Nutt.) D. Don [*Centaurea americana* Nutt.], American basketflower or star-thistle, rare annual herb, DSC, DAR, 3550–4420 ft; *JF 507a, 843* (SRSC).

Porophyllum scoparium A. Gray, Shrubby poreleaf, occasional subshrub, DSC, DAR, DCA, RIO, 1800–4000 ft; *BRM 3132, 3227, CMR 11592, SMU 38* (BGWMA); *JEA & TJW 170, JF 332, 471, 645, 1379, 2081, BGH 633, OES 1351, MT 184, BHW 18396, 20618, 21191* (SRSC); *BA2 & TE 5336, BA2 & DG 5207, DSC & HBC 30633, DF 51* (TEX-LL).

Psilostrophe gnaphalioides DC., Cudweed paperflower, rare to "infrequent" perennial herb, DSC, 1900 ft; *JF 2044, BHW 20627* (SRSC).

Psilostrophe tagetina (Nutt.) Greene var. *cerifera* (A. Nels.) B.L. Turner, Wooly paperflower, uncommon perennial herb, DSC, DAR, 2300–3560 ft; *JF 523, 605, 855, MT 17, 18, BHW 10788, 18390, GLW 4470* (SRSC); *BA2 & TE 5362, TRV 85-37* (TEX-LL).

+ *Senecio flaccidus* Less. var. *flaccidus*, [*Senecio douglasii* DC.], Threadleaf groundsel, rare perennial herb, DSC, DAR, 2400–3560 ft; *JF 513, 1431* (SRSC).

*§ *Sonchus asper* (L.) Hill, Prickly sow thistle, annual herb, RIO, 1800 ft; *BA2 4320* (BIBE).

*§ *Sonchus oleraceus* L., Sow-thistle, "frequent" annual herb, RIO; *BHW 733* (BIBE & TEX-LL); *HTF 209* (SRSC).

+ *Stephanomeria pauciflora* (Torr.) A. Nelson, Brownplume wirelettuce, rare perennial herb, DCA, 2350 ft; *JF 1358* (SRSC).

§ *Symphyotrichum divaricatum* (Nutt.) G.L. Nesom, [*Symphyotrichum subulatum* var. *ligulatum* (Shinners) S.D. Sundb.], Southern saltmarsh aster, annual herb; *EGM 134, BHW 730* (BIBE).

Symphyotrichum expansum (Poepp. ex Spreng.) Nesom, [*Symphyotrichum subulatum* var. *ligulatum* (Shinners) S.D. Sundb.], Southwestern saltmarsh aster, occasional annual herb, RIO, 1800 ft; *JF 2037, BHW 13044* (SRSC).

Tetraneuris scaposa (DC.) Greene var. *scaposa*, Stemmy four nerve daisy, occasional perennial herb, DSC, DAR, DCA, 2150–5840 ft; *CMR 5088* (BGWMA); *BHW 12895* (BIBE); *JF 258, 524a, 614, 739, 755, 1052, 1234, 1247, 1374, 1403, 1970, MT 79, 233, BHW 10850, 12895, BHW & LCH BG-67* (SRSC); *BA2 & TE 5300, 5434, BHW 12895* (TEX-LL).

§ *Thelesperma filifolium* (Hook.) Gray, Stiff greenthread, annual herb, 3520 ft; *ACK 826* (BIBE).

Thelesperma longipes A. Gray, Longstalk greenthread, occasional perennial herb, DSC, DAR, DCA, SYG, CHP, 1800–5150 ft; *BRM 3140*; *CMR 5083, 16949* (BGWMA); *BHW 12892* (BIBE, SRSC, & TEX-LL); *JF 761, 1233, 1394, 2125, BHW & LCH BG-73* (SRSC); *BA2 & TE 5325, OES 734, BHW & LCH BG-73* (TEX-LL).

Thelesperma megapotamicum (Spreng.) Kuntze var. *megapotamicum*, Rayless greenthread, uncommon perennial herb, DSC, DAR, DCA, RIO, SYG, 1800–4800 ft; *CMR 5084* (BGWMA); *JF 164, 262, 263, 1389, 2167* (SRSC); *DSC & HBC 30634, JAM & JAS 3429, AMP & SAP 3610* (TEX-LL).

§ *Thelesperma megapotamicum* (Spreng.) Kuntze var. *ambiguum* Gray, Colorado greenthread, occasional perennial herb, DAR, DCA, RIO, 1800 ft; *AMP & SAP 3610, BHW 21189, GLW 4476* (SRSC).

● *Thelesperma simplicifolium* Gray, Slender greenthread, uncommon perennial herb, DCA, 1900–4180 ft; *CMR 324, OCW 3243, BHW & LCH BG-68* (BGWMA); *JF 865, MT 63, 151, 163, AMP & SAP 5135, OCW 324, BHW 21185, BHW & LCH BG-68* (SRSC).

Trixis californica Kellogg var. *californica*, American trixis, occasional shrub, DSC, DAR, DCA, 1800–4160 ft; *JF 473, 649, 1062, 1079, 1314, 2003, 2114, BHW 10751, GLW 4455* (SRSC); *BA2, DG, & TE 5493* (TEX-LL).

Verbesina encelioides (Cav.) Benth. & Hook. f. ex A. Gray, Golden crownbeard, uncommon annual herb, DCA, RIO, 1000–2560 ft; *EGM 138, OES 746* (BIBE); *JF 1066, 2036* (SRSC).

Viguiera dentata (Cav.) Spreng., Sunflower goldeneye, uncommon to "frequent and widespread" perennial herb, DAR, SYG, CHP, 3500–5150 ft; *BHW & LCH BG-15* (BGWMA); *JF 291, 759, 1028, 1224, MT 234, BHW & LCH BG-155* (SRSC).

Viguiera stenoloba S.F. Blake, Skeletonleaf goldeneye, common shrub, DSC, DAR, DCA, SYG, CHP, 1800–5000 ft; *TR 56, CMR 16939, BHW & LCH BG-86* (BGWMA); *JF 260, 1029, 1370, 2140, TR 56, MT 145, 173, BHW & LCH BG-86* (SRSC); *BA2 & TE 5302* (TEX-LL).

§ *Xanthisma spinulosum* (Pursh) D.R. Morgan & R.L. Hartman var. *spinulosum*, [*Haplopappus spinulosus* (Pursh) DC.; *Machaeranthera pinnatifida* (Hook.) Shinners], Lacy tansyaster, cutleaf goldenweed, "fairly common" perennial herb, DSC, DAR; *GLW 4469* (SRSC); *BA2 & TE 5389, BA2 & DG 5272* (TEX-LL).

Xanthisma spinulosum (Pursh) D.R. Morgan & R.L. Hartman var. *chihuahuanum* (B.L. Turner & R. L. Hartman) D.R. Morgan & R.L. Hartman, [*Machaeranthera pinnatifida* var. *chihuahuana* B.L. Turner & Hartman], Lacy tansyaster, occasional perennial herb, DSC, DCA, RIO, 2300–3050 ft; *JF 800, 958, 1130, 1373, MT 207, 210, BHW 18391* (SRSC); *RLH & JDB 3504b, 3503* (TEX-LL).

Xylothamia triantha (Blake) Nesom, [*Ericameria triantha* (S.F. Blake) Shinners], Trans-Pecos desert goldenrod, rare subshrub, DSC, DAR, 2400 ft; *JF 1450* (SRSC).

Zinnia acerosa (DC.) A. Gray, Spinyleaf zinnia, common perennial herb, DSC, SYG, 2760–4400 ft; *BRM 3228, BHW & LCH BG-142* (BGWMA); *JF 153, 851, 1094, 1180, MT 5, 59, BHW 10837, BHW & LCH BG-142* (SRSC); *BH2 & TE 5294, BHW 10837* (TEX-LL).

Berberidaceae

+ *Berberis trifoliolata* Moric., Agarita, algerita, uncommon to occasional shrub, DSC, DAR, DCA, SYG, 2880–4600 ft; *JF 508, 528, 1001, 1036* (SRSC).

Bignoniaceae

Chilopsis linearis (Cav.) Sweet, Desertwillow, uncommon shrub or tree, DCA, 1800–4280 ft; *TR 140* (BGWMA); *BA2 5234* (SAT); *JF 1355, 1356, 2137, TR 140, MT 189* (SRSC).

Tecoma stans (L.) Juss. ex Kunth, Yellow bells, occasional shrub, DSC, DAR, DCA, 1800–3050 ft; *TR 141* (BGWMA); *BA2 5331* (SAT); *JF 179, 1010, TR 141, MT 11 193, BHW & LCH BG-85, BHW & MCJ 16866* (SRSC); *BLT & MT2 97-347, BHW & LCH BG-85* (TEX-LL).

Boraginaceae

● *Antiphytum heliotropioides* A. DC., Mexican saucerflower, rare to "locally common" shrub, DAR, DCA, 4200–4350 ft; *BA2 5220, 5313, 5453, 5465, 5600* (SAT); *JF 1936* (SRSC).

+○ *Cryptantha albida* (Kunth) I.M. Johnst., New Mexico cryptantha, rare annual herb, DCA, 1920–3000 ft; *JF 646, 805* (SRSC).

Cryptantha angustifolia (Torr.) Greene, Panamint cryptantha, rare annual herb, DSC, 2560–3560 ft; *JF 522* (SRSC); *RRI 552* (TEX-LL).

Cryptantha coryi I.M. Johnst. [*Cryptantha palmeri* (A. Gray) Payson],Cory cryptantha, rare subshrub, DSC, 3560 ft; *JF 280* (SRSC); *BLT & BD 23-164* (TEX-LL).

#Δ○ *Cryptantha crassisepala* (Torr. & A. Gray) Greene, Thicksepal catseye, annual herb, 1800 ft at the Boquillas Canyon restoration site.

§ *Cryptantha mexicana* (Brandegee) I.M. Johnst., Mexican cryptantha, "infrequent" annual herb, 2300 ft; *OCW 506* (SRSC).

Heliotropium confertifolium (Torr.) Torr. ex A. Gray, Leafy heliotrope, occasional subshrub, DSC, 1800–3800 ft; *EGM 147, BHW 907, 940* (BIBE); *JF 155, 367, BHW s.n., 940, 10848, BHW & LCH BG-76* (SRSC); *BHW s.n., 10848; BHW & LCH BG-76* (TEX-LL).

Heliotropium convolvulaceum (Nutt.) A. Gray, Phlox heliotrope, locally common annual herb, RIO, DSC, 1800 ft; *BA2, DG, TE, & PC 4608, BHW 13029* (BIBE); *WRC & PM212200, JF 2232, AMP & SAP 5860, BHW 686, 13029, 16851, GLW 4474* (SRSC); *DSC & HBC 30631, BHW 686* (TEX-LL).

Heliotropium curassavicum L. var. *curassavicum*, Salt heliotrope, locally common subshrub, RIO, 1800 ft; *EGM 124, 943, CN 495* (BIBE); *JF 2256, BCT 8802* (SRSC); *BCT 8802, BHW 943* (TEX-LL).

#Δ *Heliotropium glabriusculum* (Torr.) A. Gray, Greeneye heliotrope, perennial herb, 1800 ft, head of Boquillas Canyon.

§ *Heliotropium greggii* Torr., Fragrant heliotrope, perennial herb, 1800 ft; *DSC & IMJ 21926* (SRSC).

§ *Heliotropium procumbens* Mill., Fourspike heliotrope, subshrub; *BHW 1089* (TEX-LL).

Lappula redowskii (Hornem.) Greene,[*L. occidentalis* (S. Wats.) Green] Flatspine stickseed, occasional annual herb, DAR, DCA, 1800–3560 ft; *DB 22, TK 10, BRM 3124* (BGWMA); *JF 427, 540a, 797, 2101, BHW 47057, 47059* (SRSC).

+● *Lithospermum incisum* Lehm., Fringed puccoon, narrowleaf stoneseed, rare perennial herb, SYG, 4360–4800 ft; *BA2 5539, 5597* (SAT); *JF 554, 1948* (SRSC).

§ *Omphalodes aliena* A. Gray ex Hemsl., Mexican navelwort, "frequent" annual herb, DSC, DCA, RIO, 1800–2560 ft; *BRM 3131* (BGWMA); *JLB 1578, ECM 49* (SAT); *AMP 5367, BHW 15991, 18395* (SRSC); *DSC & WOD 30715* (TEX-LL).

§ *Tiquilia canescens* (DC.) A.T. Richardson var. *canescens*, Woody crinklemat, occasional subshrub, DSC, 2200–2400 ft; *BA2 5340* (SAT); *TR 4* (SRSC); *TR 4, BHW 1230* (TEX-LL).

Tiquilia gossypina (Wooton & Standl.) A.T. Richardson, Texas crinklemat, occasional subshrub, DSC, DCA, 1800–3440 ft; *JF 360, 2059, BHW 12899* (SRSC); *BHW 909* (TEX-LL).

Tiquilia greggii (Torr.) A.T. Richardson, Plume tiquilia, occasional shrub, DSC; *CMR 11634* (BGWMA); *BA2 5270* (SAT); *JF 359, 369; MT 213, BHW 10800* (SRSC).

§ *Tiquilia hispidissima* (Torr.) A.T. Richardson, Rough coldenia, occasional subshrub, DSC, 1850–3520 ft; *BA2, DG, TE, & B 4923, ACK 822, BHW 908, 909* (BIBE); *BLT & BD 23-162, BHW 21682, 21692* (TEX-LL).

Tiquilia mexicana (S. Watson) A.T. Richardson, Mexican crinklemat, occasional subshrub, 1800–3400 ft; *JF 152a, 812, 1443, BHW 13072, 23038, GLW 4487* (SRSC).

Brassicaceae

Descurainia pinnata (Walter) Britton, Tansymustard, uncommon annual herb, DSC, DAR, DCA, 3440–3500 ft; *BA2 5587* (SAT); *JF 422, 617* (SRSC).

§ *Dimorphocarpa wislizeni* (Engelm.) Rollins, Spectacle pod, touristplant, locally common annual herb, DCA, 3500 ft; *BHW 47060* (SRSC & TEX-LL); *VLC 43958, RRI 558* (TEX-LL).

Draba cuneifolia Nutt. ex Torr. & A. Gray, Wedgeleaf draba, occasional annual herb, DSC, DAR, DCA, SYG, 1800–5080 ft; *JF 429, 536, 566, 738, 802, BHW 18392, BHW & MCJ 15990* (SRSC); *BHW & MCJ 15990* (TEX-LL).

§ *Lepidium alyssoides* A.Gray var. *angustifolium* (C.L. Hitchc.) Rollins, Mesa pepperwort, perennial herb; *HBP 1923* (TEX-LL).

Lepidium lasiocarpum Nutt. ex Torr. & A. Gray var. *wrightii* (A. Gray) Thell., Wright pepperweed, uncommon annual herb, DAR, DCA, 3440–3560 ft; *JF 619* (BIBE); *BA2 734, 5540, 5586; RE 734* (SAT); *JF 421, 565, 619* (SRSC).

Nerisyrenia camporum (A. Gray) Greene, Bicolored mustard, common perennial herb, DSC, DCA, SYG, 2120–4280 ft; *CMR*

16047 (BGWMA); *JF 492* (BIBE); *JF 372, 492, 615, 681, MT 105BHW 208, 47054, BHW & HKB 47063* (SRSC); *BHW T208, 47063* (TEX-LL).

Physaria fendleri (A. Gray) O'Kane & Al-Shehbaz, Fendler bladderpod, occasional perennial herb, DSC, DAR, DCA, SYG, 2200–5000 ft; *JF 557* (BIBE); *TR 105* (BGWMA); *JF 200, 497a, 555, 557, 736, 1189, TR 139, MT 75, 104, BHW 47062* (SRSC).

+ *Physaria gordonii* (A. Gray) O'Kane & Al-Shehbaz, Gordon bladderpod, rare annual herb, SYG, 4360 ft; *JF 570* (SRSC).

Physaria mcvaughiana (Rollins) O'Kane & Al-Shehbaz, Mcvaugh bladderpod, rare perennial herb, SYG, 4120–5840 ft; *JF 497, 714, 1535, 1964, AMP & SAP 5133* (SRSC).

§ *Physaria purpurea* (Gray) O'Kane & Al-Shehbaz [*Lesquerella purpurea* (A. Gray) S. Watson], Rose bladderpod, "frequent" perennial herb; *BHW & MCJ 15995* (SRSC).

Schoenocrambe linearifolia (A. Gray) Rollins, Slimleaf plain-smustard, rare perennial herb, SYG, 3500–5680 ft; *BRM 3110* (BGWMA); *JF 734, 1291, 2185, MT 42, 43, 246, BHW & LCH BG-154* (SRSC).

§ *Selenia dissecta* Torr. & A. Gray, Texas selenia, "frequent" annual herb, DCA, 3500 ft; *CMR 16410* (BGWMA); *BHW 47058, BHW & MCJ 15989* (SRSC); *BHW 47058* (TEX-LL).

*§● *Sisymbrium irio* L., London rocket, annual herb, DCA, 2560 ft; *RRI 551* (TEX-LL).

Streptanthus cutleri Cory, Cutler twistflower, uncommon (G2S2) biennial herb, DSC, DAR, DCA, 1800–3500 ft; *JF 420, AMP 3570, 5366, AMP & SAP 4299, 5387, BHW 18399, BHW & MCJ 15992* (SRSC).

§ *Thelypodium texanum* (Cory) Rollins, Texas thelypody, annual herb; *OES 1288* (SRSC).

§ *Thelypodium wrightii* A. Gray, Wright thelypody, perennial herb, DCA; *BRM 3106* (BGWMA).

Cactaceae

Ariocarpus fissuratus (Engelm.) K. Schum., Living rock cactus, common succulent, DSC, SYG, 3350–ca. 4500 ft; *BA2 5278, DB 468* (SAT); *JF 274, 1479, DS2 12b* (SRSC).

§ *Coryphantha dasyacantha* (Engelm.) Orcutt., Desert pincushion cactus, succulent, 4125 ft; *MT 90* (SRSC).

Coryphantha duncanii (Hester) L.D. Benson, [*Escobaria dasyacantha* var. *duncanii* (Hester) N.P. Taylor], Duncan cory cactus, rare (G3T1T2S1S2) succulent, DSC, ca. 2000–4146 ft; *JF 549, JF & MD 612, AMP 5373, DS2 2228* (SRSC).

Coryphantha echinus (Engelm.) Britton & Rose var. *echinus*, [*Mammillaria scolymoides* Scheidw.], Sea-urchin cactus, occasional succulent, rocky soils, open desert and slopes, DSC, SYG, 3500–4360 ft; *JF 593, 868, 1493, BHW 11061* (SRSC).

Coryphantha echinus (Engelm.) Britton & Rose var. *robusta* A.M. Powell, Multi-stemmed sea-urchin cactus, rare succulent, DSC, 2400–3650 ft; *JF 1440, 1494* (SRSC).

Coryphantha sneedii (Britton & Rose) A. Berger var. ***albicolumnaria*** (Hester) A.D Zimmerman, Silverlace cactus, [*Coryphantha albicolumnaria* (Hester) Zimmerman; *Corphantha sneedii* var. *albicolumnaria* (Hester) A.D. Zimmerman (forthcoming, cited in Powell and Weedin 2004); *Escobaria albicolumnaria* Hester], rare (G2G3S2S3) succulent, DSC, SYG, 1800–4840 ft; *DAZ 1541* (BIBE); *JF 556, 587, 588* (SRSC).

Coryphantha tuberculosa (Engelm.) A. Berger var. *tuberculosa*, [*Mammillaria tuberculosa* Engelm.], Cob cactus, common succulent, DSC, DCA, SYG, 1900–5840 ft; *CMR s.n.* (BGWMA); *JF 273, 386, 550, 625, 781, 1300, MT 89* (SRSC).

§ *Coryphantha tuberculosa* (Engelm.) A. Berger var. *varicolor* (Tiegel) A.D. Zimmerman, [*Coryphantha dasyacantha* var. *varicolor* (Tiegel) L.D. Benson], Varicolor cob cactus, succulent; *BA2 471* (SAT).

Echinocactus horizonthalonius Lem., Eagle claw cactus, occasional succulent, DSC, DCA, SYG, 4360 ft; *CMR 5173* (BGWMA); *DB 470* (SAT); *JF 591* (SRSC).

Echinocereus dasyacanthus Engelm., Rainbow cactus, common succulent, DSC, SYG, 1900–5700 ft; *DB 469* (SAT); *JF 558, 623* (SRSC).

+ *Echinocereus enneacanthus* Engelm. var. *enneacanthus*, Strawberry cactus, occasional succulent, DSC, 1800 ft; *JF 2148* (SRSC).

+○ *Echinocereus stramineus* (Engelm.) Rumpler var. *stramineus*, Strawberry pitaya, common succulent, DSC, DCA, SYG, 1800–4440 ft; *JF 780, 2149* (SRSC).

Echinomastus mariposensis Hester, [*Neolloydia mariposensis* (Hester) L.D. Benson; *Sclerocactus mariposensis* (Hester) N.P. Taylor], Mariposa cactus, occasional (G2S2; LT/T) succulent, DSC, DCA, 3300–3520 ft; *CMR 5172* (BGWMA); *JF 391, 624, AMP & SAP 5925, DS2 2221* (SRSC).

Echinomastus warnockii (L.D. Benson) Glass & R. Foster, [*Sclerocactus warnockii* (L.D. Benson) N.P. Taylor], Warnock cactus, occasional succulent, DSC, DCA, 1900–2560 ft; *JF 2150, BHW 47459, BHW & HKB 47012* (SRSC).

+ *Epithelantha micromeris* (Engelm.) F.A.C. Weber ex Britton & Rose, Common button cactus, uncommon succulent, DSC, SYG, 3560–4140 ft; *JF 268a, 271, 586, 613, 613a, 1486* (SRSC).

Ferocactus hamatacanthus (Muehlenpf.) Britton & Rose var. *hamatacanthus*, Giant fishhook cactus, occasional succulent, DCA, SYG, 4300–4900 ft; *CMR 5174* (BGWMA); *JF 590, 1507, MT 96* (SRSC).

Glandulicactus uncinatus var. *wrightii* (Engelm.) Backeb., [*Ancistrocactus uncinatus* var. *wrightii* (Engelm.) L.D. Benson; *Echinocactus uncinatus* Galeotti ex Pfeiff.; *Ferocactus uncinatus* (Galeotti ex Pfeiff.) Britton & Rose], Eagle claw cactus, uncommon succulent, DSC, SYG, 3520–4040 ft; *DS2 03b, JF 548* (SRSC).

§ *Mammillaria heyderi* Muehlenpf. var. *heyderi*, Heyder pincushion cactus, "rare" succulent, DSC, 2500 ft; *AMP, SAP, MLP, & AL2 6103* (SRSC).

§ *Mammillaria lasiacantha* Engelm., Golf ball cactus, succulent, DSC, ca. 3520 ft; *DS2 18b, 2222, JFW s.n.* (SRSC).

§ *Mammillaria meiacantha* Engelm., Nipple cactus, succulent; *BHW 11065* (SRSC).

Neolloydia conoidea (DC.) Britton & Rose, Texas cone cactus, occasional to locally abundant succulent, SYG, 3080–5200 ft; *JF 380, 782, DS2 2220, MT 52, 53, 122, BHW 11055, 11058* (SRSC).

Opuntia aggeria Ralston & Hilsenb., Clumped dog cholla, common succulent at lower elevations, DSC, 1850–300 ft; *JF 635, 640, 691, 704, 1562, 1563, 1574, 1574a, 1576, 1620, BAR & RAH 136* (SRSC).

Opuntia azurea Rose var. ***aureispina*** (S. Brack & K.D. Heil) A.M. Powell & J.F. Weedin, [*Opuntia aureispina* (S. Brack & K.D. Heil) Pinkava & B.D. Parfitt], Golden-spined prickly pear, G1S1 succulent, RIO, 1800 ft; *JF 384, BGH 802* (SRSC).

+ *Opuntia camanchica* Engelm. & J.M. Bigelow, Comanche prickly pear, succulent, DSC, DAR, 3560 ft; *MA 848, JF 626* (SRSC).

§ *Opuntia densispina,* Densely-spined dog cholla, succulent; *DOK & JFW 53, AMP & SAP 6275* (SRSC).

Opuntia dulcis Engelm., Sweet prickly pear, succulent, DSC, 1800–3560 ft; *JF* 628; *AMP & SAP 6278; MPG 87, 88, 89* (SRSC).

+o *Opuntia engelmannii* Salm-Dyck ex Engelm. var. *engelmannii,* Engelmann prickly pear, uncommon succulent, SYG, 4440 ft; *JF 589* (SRSC).

§ *Opuntia engelmannii* var. *lindheimeri* (Engelm.) B.D. Parfitt & Pinkava, Texas prickly pear, succulent, DSC, 1800 ft; *AMP & SAP 6277, JFW 1171* (SRSC).

*§ *Opuntia ficus-indica* (L.) Mill., Indian fig, rare succulent; *BGH 646* (SRSC).

Opuntia grahamii Engelm., Graham dog cholla, occasional succulent, DSC, 3000–3520 ft; *CMR 5178* (BGWMA); *MA 892* (BIBE); *JF 333, 377, 378, 389, 783, 892, 1142a* (SRSC).

Opuntia kleiniae DC., Candle cholla, occasional succulent, RIO, 1800 ft; *BGH 841, JF 2040* (SRSC).

Opuntia leptocaulis DC., Tasajillo, christmas cactus, occasional succulent, DSC, DAR, 3360–4120 ft; *JF 388, 448, 816, WH, TA, LS & JMP 9028* (SRSC).

Opuntia rufida Engelm., Blind prickly pear, common succulent, DSC, DAR, DCA, 1800–3560 ft; *JF 627, BGH 803, WH, TA, LS & JMP 8985* (SRSC).

Opuntia spinosibacca M.S. Anthony, Spiny-fruited prickly pear, succulent, DSC, 1800–4600 ft; *MA A-3, A-7, JF 385, BGH 801, 842, AMP & SAP 5824, 6089* (SRSC).

Opuntia sp., Prickly pear; *BGH 800, 840; AMP & SAP 6276* (SRSC).

Capparidaceae

Koeberlinia spinosa Zucc., Allthorn, occasional shrub, DSC, DAR, DCA, 2500–3800 ft; *WFM s.n., CMR 32* (BGWMA); *JF 1441, JF & HL 1891, MT 8* (SRSC).

Caprifoliaceae

Lonicera albiflora Torr. & A. Gray, Western white honeysuckle, rare perennial woody vine, SYG/CHP, DCA, 4280–5680 ft; *BRM 3230* (BGWMA); *PVW s.n.* (KANU); *BA2 5436* (SAT); *JF 1296, AMP & SAP 5125* (SRSC).

Caryophyllaceae

§ *Arenaria benthamii* Fenzl ex Torr. & A. Gray, Hilly sandwort, annual herb; *BRM s.n.* (BGWMA).

Paronychia jamesii Torr. & A. Gray, James nailwort, uncommon perennial herb, DSC, SYG, 3800–5800 ft; *BA2 5475* (SAT); *JF 235, 765, 1269a, MT 33, 248* (SRSC).

Celastraceae

Mortonia scabrella A. Gray, Tickbush, Rio Grande saddlebush, sandpaper bush, uncommon shrub, DSC, SYG, 3840–5000 ft; *PVW s.n.* (KANU); *JF 268, 1167, 2190, MT 2* (SRSC).

Schaefferia cuneifolia A. Gray, Desert yaupon, occasional shrub, DSC, DAR, DCA, 1900–3300 ft; *TR 126* (BGWMA); *JF 676, 973, 1366, 2041, AMP & SAP 4302, BHW 15912* (SRSC); *AMP & SAP 4302* (TEX-LL).

Chenopodiaceae

Atriplex canescens (Pursh) Nutt. var. *canescens,* Fourwing saltbush, uncommon shrub, DSC, DAR, DCA, SYG, 1800–4160 ft; *BA2 5262* (SAT); *JF 336, 861, 1091, 1410, 1895, 2143, MT 203, BHW & LCH BG-132* (SRSC); *BHW & LCH BG-132* (TEX-LL).

*◆ *Atriplex rosea* L., Tumbling saltweed, red orache, rare annual herb, RIO, 1800 ft; *AL 306* (BIBE); *AL 307, JF 2236* (SRSC).

Chenopodium berlandieri Moq., Pitseed goosefoot, rare annual herb, DAR, RIO, 1800–3440 ft; *JF 361, 616, 2122, 2238* (SRSC).

Corispermum americanum (Nutt.) Nutt., American bugseed, locally common annual herb, DSC, RIO, 1800–2100 ft; *BHW 8330, JF 2221, 2224* (SRSC); *DSC & HBC 30630, BHW 8330* (TEX-LL).

!# *Salsola tragus* L., Tumbleweed, locally common annual herb, RIO, 1800 ft; *JF 2252* (SRSC).

Suaeda suffrutescens S. Watson var. *suffrutescens,* [*Suaeda nigra* (Raf.) J.F. Macbr.], Desert seepweed, rare perennial subshrub, RIO, 1800 ft; *JF 2234* (SRSC).

Convolvulaceae

§ *Bonamia ovalifolia* (Torr.) Hallier f., Bigpod lady's nightcap, "locally common" subshrub, DSC, RIO, 1800 ft; *BA2, DG, TE, & PC 4551; JS 303* (BIBE); *HBC 30628* (NYBG); *BA2 5502* (SAT); *BGH 622, DAL 40, AMP 3347, AMP & JH 5696, AMP & SAP 3609, 5859, GLW 4482* (SRSC); *DSC & HBC 30628, AMP 3347, AMP & SAP 3609* (TEX-LL).

Bonamia repens (I.M. Johnst.) D.F. Austin & Staples, Creeping lady's nightcap, common subshrub, DSC, DAR, 1800–4280 ft; *CA & BA2 69, BA2 6191, SMU 41* (BGWMA); *CA s.n.* (SAT); *JF 154, 307, 435, 1075, 2062, 2131, MT 167, BHW & MCJ 16834* (SRSC).

Convolvulus equitans Benth., Texas bindweed, uncommon perennial herbaceous vine, DAR, DCA, RIO, 1800–4350 ft; *BRM 3149* (BGWMA); *JF 1945, EGM 150* (BIBE); *BA2 5309, 5470, 5720* (SAT); *JF 181, 853, 1349, 1432, 1945, 2077, 2116* (SRSC).

Dichondra brachypoda Wooton & Standl., New Mexico ponysfoot, rare perennial herb, DAR, DCA, 3056–4600 ft; *JF 859, 1122, AMP & SAP 5134* (SRSC).

Evolvulus alsinoides (L.) L. var. *angustifolius* Torr., Slender dwarf morning-glory, occasional perennial herb, DSC, DAR, DCA, 1900–3880 ft; *TR 249* (BGWMA); *BA2 5312, 5464* (SAT); *JF 209, 309, 957, 1472, 2060, TR 250; MT 127* (SRSC).

§ *Ipomoea cardiophylla* A. Gray, Heartleaf morning-glory, rare annual vine; *BHW 10799* (SRSC).

Ipomoea costellata Torr., Crest-rib morning glory, rare but locally common perennial herbaceous vine, SYG, 5300–5840 ft; *JF 1994* (BIBE); *JF 1969, 1994, MT 241* (SRSC).

§ *Ipomoea lindheimeri* A. Gray, Lindheimer morning-glory, "infrequent" perennial herbaceous vine, 3520 ft; *MA & AD 874* (SRSC).

Ipomoea rupicola House, Cliff morning-glory, occasional to uncommon perennial herbaceous vine, DSC, DAR, DCA, SYG,

3050–4800 ft; *JF 248* (BIBE); *JF 248, 308, 1103, 1186, 1196, MT 31, 144, 172, BHW 962, BLT & BD 23-167, OCW 352, BHW & LCH BG-148, BHW & MCJ 16828* (SRSC); *BLT & BD 23-167* (TEX-LL).

§ *Ipomoea tenuiloba* Torr., Spiderleaf, rare perennial herbaceous vine; *MT 236* (SRSC).

Crassulaceae

Echeveria strictiflora A. Gray, Siempreviva, desert savior, rare succulent, SYG/CHP, 5700–5840 ft; *BRM 3224* (BGWMA); *JF 1263, 1301, BHW 10774* (SRSC).

Sedum nanifolium Fröd., [*Sedum robertsianum* Alexander; *Sedum parvum* Hemsl. subsp. *robertsianum* (Alexander) R.T. Clausen], Dwarf stonecrop, rare but locally occasional succulent, SYG, 5150 ft; *JF 1215* (BIBE & SRSC).

Sedum wrightii A. Gray, Wright stonecrop, rare succulent, SYG, 4200–5000 ft; *JF 581, 1163, 1506* (SRSC).

Crossosomataceae

Glossopetalon spinescens A. Gray var. *spinescens*, [*Forsellesia spinescens* (A. Gray) Greene], Spiny greasebush, uncommon shrub, SYG, 4200–5000 ft; *PVW s.n.* (KANU); *JF 1205, 1505, BHW 10843* (SRSC).

Cucurbitaceae

Ibervillea lindheimeri (A. Gray) Greene, Lindheimer globeberry, rare perennial herbaceous vine, DSC, 3080 ft; *JF 1143* (SRSC).

§ *Ibervillea tenuisecta* (A. Gray) Small, Slimlobe globeberry, uncommon perennial herbaceous vine, DSC, 3500–3800 ft; *BA2 5368* (SAT); *MA & AD 3500, BHW 10802, MT 206* (SRSC); *BHW 10802* (TEX-LL).

Ebenaceae

Diospyros texana Scheele, Texas persimmon, common to occasional shrub, DAR, DCA, 1800–3840 ft; *BRM 3146, CMR 5080* (BGWMA); *BA2 5239, MC 157, CMR 15102* (SAT); *JF 689, 2088, WH, TA, LS, & JMP 8986* (SRSC).

Euphorbiaceae

Acalypha monostachya Cav., [*Acalypha hederacea* Torr.], Round copperleaf, common perennial herb, DSC, DAR, DCA, 1850–3050 ft; *BA2 5237, 5334* (SAT); *JF 1069, 1118, 1680, BHW 646, 21200* (SRSC); *BHW 646* (TEX-LL).

Acalypha phleoides Cav., [*Acalypha lindheimeri* Müll. Arg.], Shrubby copperleaf, occasional perennial herb, DAR, DCA, 2200–4800 ft; *JF 1946* (BIBE); *TR 68, CMR 11583* (BGWMA); *BA2 5240, 5265* (SAT); *JF 1108, 1128, 1149, 1946, JF & MY 1315, TR 68, MT 187* (SRSC); *OCW s.n.* (TEX-LL).

Andrachne arida (Warnock & M.C. Johnst.) G.L. Webster, Trans-Pecos maidenbush, rare but locally common (G2S1) shrub, SYG, 4200–4900 ft; *JF 1170, 1194, 1207, 1499, 2164, 2177, BHW 10767, 1077; BHW & MCJ 16681, 16840, 16841* (SRSC).

Bernardia obovata I.M. Johnst., Desert myrtlecroton, occasional shrub, DSC, DAR, DCA, 1920–4900 ft; *CMR 5134, BHW & LCH s.n.* (BGWMA); *BA2, DG, TE, & B 4925* (BIBE); *BA2 5250, BR 293* (SAT); *JF 203, 496, 642, 715, 1093, 1212, MT 86, BHW 10832, BHW & LCH BG-178, BHW & MCJ 16833* (SRSC); *BHW 10832, BHW & LCH BG-178* (TEX-LL).

Chamaesyce acuta (Engelm.) Millsp., Pointed sandmat, rare perennial herb, SYG, 5700 ft; *JF 1264* (SRSC).

Chamaesyce albomarginata (Torr. & A. Gray) Small, Whitemargin sandmat, uncommon perennial herb, DSC, DAR, 1800–2560 ft; *JF 1447* (SRSC); *HBP & VLC 30177, OES 1540* (TAES).

Chamaesyce chaetocalyx (Boiss.) Wooton & Standl., Bristlecup sandmat, locally common subshrub, DSC, DCA, 1960–4600 ft; *BHW & LCH s.n.* (BGWMA); *JF 261, 652, 943, AMR & SAP 5142, MT 32, 68, BHW & LCH BG-176* (SRSC).

Chamaesyce cinerascens (Engelm.) Small, Ashy sandmat, occasional perennial herb, DSC, DAR, DCA, SYG, 1800–4450 ft; *OCW s.n.* (BGWMA); *BA2, DG, TE, & B 4934* (BIBE); *BA2 5291, 5526, 5705* (SAT); *JF 174, 340, 342, 489, 547, 653, 684, 863, 1078, 1087, 1171, 1337, 2133, 1645, AMP & SAP 3612, 5305, AMP, SAP, MLP, & AL2 6101, MT 3, 66, 67, 165, 166, BLT 22-146, BHW 10756, 10762, 10840, 18393, BHW & LCH BG-66, BHW & MCJ 15908, GLW 4442* (SRSC); *DSC & HBC 30632, BLT 22-146, BHW 10756, 10762, BHW & LCH BG-66* (TEX-LL).

Chamaesyce fendleri (Torr. & A. Gray) Small, Fendler sandmat, uncommon perennial herb, DSC, SYG, CHP, 3000–5250 ft; *JAM & JAS 3444* (NYBG); *BA2 5210, 5276, 5619, 5692* (SAT); *JF 784, 1235, 1243, 1470, 2197* (SRSC).

Chamaesyce glyptosperma (Engelm.) Small, Rib-seed sandmat, "frequent" annual herb, RIO, DSC, 1800–3120 ft; *JF 223, BHW & BLT 8317* (SRSC); *BHW & BLT 8325* (TEX-LL).

§ ***Chamaesyce golondrina*** (L.C. Wheeler) Shinners, Boquillas sandmat, rare but locally frequent (G2S2) annual herb, DSC, ca. 1800 ft; *AL 175, BHW 998* (BIBE); *WRC & PM212199, AMP & SAP 3613, BHW 20900, 20951, 20954, 23035, BHW & MCJ 16854, BHW & BLT 8325a, 8325b, GLW 4484* (SRSC); *AMP & SAP 3613* (TEX-LL).

+ *Chamaesyce serpens* (Kunth) Small, Matted sandmat, rare annual or perennial herb, DSC/DAR, 2400 ft; *JF 1422* (SRSC).

§ *Chamaesyce serpyllifolia* (Pers.) Small, Thyme-leaf sandmat, uncommon annual herb, DSC, 3800 ft; *BHW 10794* (TEX-LL).

Chamaesyce serrula (Engelm.) Wooton & Standl., Sawtooth sandmat, uncommon but locally frequent annual herb, DSC, SYG, 1800–5100 ft; *EGM 165* (BIBE); *JF 2196, BHW 10794, 10838* (SRSC); *BHW 10838* (TEX-LL).

Chamaesyce theriaca (Wheeler) Shinners, Terlingua sandmat, Terlingua broomspurge, rare to frequent annual herb, DSC, DCA, 1800–3800 ft; *CMR 15117* (SAT); *JF 2018, 2095, AMP & SAP 6138, 6139, BHW 13033, 23402, BHW & LCH BG-180, BHW & MCJ 16678, 16680, BHW & BLT 8325, 8326* (SRSC); *BHW & BLT 8325, 8326* (TEX-LL).

Chamaesyce triligulata (L.C. Wheeler) B.L. Turner [*Chamaesyce chaetocalyx* var. *triligulata* (L.C. Wheeler) Mayfield; *Chamaesyce fendleri* (Torr. & Gray) Small var. *triligulata* (L.C. Wheeler) Shinners], Bristlecup sandmat, three-tounge spurge, rare (G5T1S1) perennial herb, DSC, DCA, 1800–2200 ft; *AL 164, 165* (BIBE); *JF 1695, AMP & SAP 3611, BHW 20899, BHW & MCJ 16960* (SRSC).

Chamaesyce villifera (Scheele) Small, Hairy sandmat, rare perennial herb, SYG, 4360–5840 ft; *JF 1173, 1305, 1960* (SRSC).

Croton bigbendensis B.L. Turner, Big Bend croton, occasional perennial herb, DSC, 3000–3880 ft; *JF 292, 707, 1463, 1904, MT 158* (SRSC); *BLT & BD 23-163* (TEX-LL).

§ *Croton dioicus* Cav., Grassland croton, hierba del gato, locally "frequent and widespread" perennial herb, DSC, 2150 ft; *EGM 144* (BIBE); *WGD s.n.* (TAES); *BHW & LCH BG-64* (SRSC & TEX-LL).

Croton fruticulosus Engelm. ex Torr., Bush croton, encinilla, occasional perennial herb, DAR, DCA, 2200–4100 ft; *BRM 3137, TR 72, 73, OCW 314* (BGWMA); *JF 298* (BIBE); *JF 298, 300, 509, 1114, TR 72, 73, MT 40, 98, 256, OCW 340, BHW 10748* (SRSC); *BHW 10748* (TEX-LL).

Croton incanus Kunth, Torrey croton, rare shrub, DCA, 1800 ft; *JF 2128, BHW 18406* (SRSC).

+ *Croton lindheimerianus* var. *tharpii* M.C. Johnst., Tharp croton, rare annual herb, DSC/DAR, 2400 ft; *JF 1427* (BIBE & SRSC).

§ *Croton pottsii* (Klotzsch) Müll. Arg., Leatherweed, perennial herb, 2200–2400 ft; *TR 71* (BGWMA & SRSC).

Croton thermophilus (M.C. Johnst.) B.L. Turner [*Croton pottsii* var. *thermophilus* (M.C. Johnst.) M.C. Johnst], Leatherweed, occasional (G5T2S1) perennial herb, DSC, DCA, SYG, 1850–4400 ft; *BRM 3113* (BGWMA); *AL 158* (BIBE); *JF 175, 353, 431, 457, 682, 1077, 1397, 1541, 1932, 2011, 2058, MT 159, BHW 18401, 20895, BHW & MCJ 16837, 16862, BHW & BLT 8321, GLW 4439* (SRSC).

Ditaxis humilis (Engelm. & A. Gray) Pax, Low silverbush, rare perennial herb, DSC, 2560–2760 ft; *JF 152, 1404, BHW & LCH BG-201* (SRSC).

Ditaxis neomexicana (Müll. Arg.) A. Heller, New Mexico ditaxis, occasional to common perennial herb, DSC, DAR, 1800–3500 ft; *CMR 5032* (BGWMA); *EGM 133, BHW 12889* (BIBE); *BA2 5319, 5584* (SAT); *JF 168, 439, 674, 2051, BLT 22-151, BHW 12889, BHW & LCH BG-199, BHW & MCJ 16858* (SRSC); *BLT 22-151, BHW 12889* (TEX-LL).

Euphorbia antisyphilitica Zucc., Candelilla, common perennial herb, DSC, DAR, DCA, SYG, 1900–4400 ft; *BA2 5241, 5695* (SAT); *JF 259, 573, 778, MT 84, 170, BHW & MCJ 16839* (SRSC); *AT 2243* (TEX-LL).

Euphorbia brachycera Engelm., Horned spurge, uncommon perennial herb, DCA, SYG/CHP, 3500–5680 ft; *JF 160* (BIBE); *BHW & LCH s.n.* (BGWMA); *BA2 2513, 5445* (SAT); *JF 1273, 1290, 1934, 1940, AMP & SAP 5141, BHW & LCH BG-174* (SRSC).

Euphorbia eriantha Benth., Desert poinsettia, beetle spurge, uncommon annual herb, DSC, 1800–1850 ft; *JF 2010, 2103; BGH 634* (SRSC).

Euphorbia exstipulata Engelm., Square-seed spurge, uncommon annual herb, DSC, SYG, 2800–5840 ft; *JF 198, 1980, BHW & MCJ 16832* (SRSC).

Jatropha dioica Cerv. var. *graminea* McVaugh, Sangre de drago, leatherstem, common perennial herb, DSC, DAR, DCA, 1800–4360 ft; *CMR 17230* (BIBE); *BA2 5479* (SAT); *JF 709, 586, 2029, BHW 12902, 13073* (SRSC).

Phyllanthus polygonoides Nutt. ex Spreng., Knotweed leafflower, occasional subshrub, DSC, DAR, DCA, 1850–4360 ft; *BHW & LCH s.n.* (BGWMA); *JF 160* (BIBE); *BA2 5206, 5292, 5593, 5693* (SAT); *JF 160, 205, 297, 526, 825, 1074, 1400, TRV s.n., BHW & LCH BG-146, BHW & MCJ 16830, GLW 4450* (SRSC).

Tragia amblyodonta (Müll. Arg.) Pax & K. Hoffm., Dogtooth noseburn, uncommon perennial herb, DSC, DAR, DCA, 2680–5680 ft; *JF 146, 718, 832, 1297, BLT 22-150, BHW & LCH BG-188* (SRSC); *BLT 22-150* (TEX-LL).

Tragia ramosa Torr., Branched noseburn, uncommon perennial herb, DSC, 2120–5840 ft; *TR 74, CMR 5085* (BGWMA); *BA2 5208, 5283, 5694* (SAT); *JF 688, 1966* (SRSC).

Fabaceae

Acacia berlandieri Benth., Guajillo, rare tree, DSC, SYG, 2520–4700 ft; *JF 669* (BIBE); *JF 669, 2187, BHW 21189b* (SRSC).

Acacia constricta Benth. ex A. Gray, Whitethorn acacia, occasional shrub or tree, DSC, DCA, 2350 ft; *CMR 11592* (BGWMA); *LF 86, PAS 58* (SHST); *JF 1385* (SRSC); *VB 355* (TEX-LL).

Acacia farnesiana (L.) Willd. [*Acacia smallii* Isely], Huisache, uncommon tree, DSC, RIO, 1800 ft; *BHW 13040* (BIBE); *JF 2030, EJL 126-H, TCM 2003-66b, PM 2037, AMP 3348, BHW 13040, 18386* (SRSC); *AMP 3348, BHW 13040* (TEX-LL).

Acacia greggii A. Gray var. *greggii*, Catclaw acacia, uncommon shrub, DSC, DAR, DCA, 2350 ft; *SJ 6505* (SAT); *JF 1372, BHW 21201, 21204* (SRSC).

Acacia neovernicosa Isely, Viscid acacia, uncommon to occasional shrub or tree, DSC, DAR, DCA, 1800–3408 ft; *EGM 149* (BIBE); *JF 934, 1089, 1462, 2020a-c, BHW 20777* (SRSC).

+ *Acacia rigidula* Benth., Blackbrush acacia, uncommon tree, DSC/ RIO, 1000–1850 ft; *JF 2002, 2027* (SRSC).

Acacia roemeriana Scheele, Roemer acacia, common shrub or tree, DSC, DAR, DCA, 1800–4180 ft; *BRM 3116, BHW & LCH s.n.* (BGWMA); *JF 249, 644, 1012, BHW & LCH BG-147* (SRSC).

§ *Acacia schottii* Torr., Schott acacia, rare shrub or tree, DSC; *BHW 20896* (SRSC).

+ *Astragalus austrinus* (Small) Schulz, Smallflowered milkvetch, rare annual or perennial herb, DSC, DAR, DCA, 3000–3560 ft; *JF 426, 540b, 804* (SRSC).

§ *Astragalus mollissimus* Torr., Woolly locoweed, perennial herb; *BA2 4755, SJ 4755* (SAT).

§• *Astragalus wrightii* A. Gray, Wright milkvetch, annual herb; *VLC 43964* (TEX-LL).

+ *Calliandra iselyi* B.L. Turner, Falsemesquite, occasional subshrub, DSC, SYG, 2800–5150 ft; *JF 813, 938, 1142, 1324, 1469* (SRSC).

§ *Cercis canadensis* L. subsp. *mexicana* (Rose) E. Murray, Mexican redbud, "infrequent" to "common" tree, 3500–4600 ft; *BA2 5232* (SAT); *AMP & SAP 5140* (SRSC), *BHW & LCH BG-172* (SRSC & TEX-LL).

§ *Dalea aurea* Nutt. ex Fraser var. *aurea*, Golden prairie clover, perennial herb; *BRM 3223* (BGWMA); *BA2 5318* (SAT).

Dalea formosa Torr., Feather dalea, plume dalea, occasional shrub, DSC, DAR, DCA, SYG/CHP, 2560–5840 ft; *CMR 17225* (BIBE); *BA2 315, 5191, 5538* (SAT); *JF 483, 559, 1014, 1047, 1096, 1402, 1914, 1996, MT 136* (SRSC); *VB 342* (TEX-LL).

Dalea frutescens A. Gray var. *frutescens*, Black dalea, uncommon shrub, DSC, DAR, DCA, SYG, 3350–5800 ft; *BA2 5484, 5332* (SAT); *JF 374a, 1195, MT 230, 245, BHW 10754* (SRSC); *BHW 10754* (TEX-LL).

Dalea greggii A. Gray, Gregg prairie clover, uncommon subshrub, DSC, SYG, 3800–4600 ft; *OCW 9022* (BGWMA); *BA2 5277, 5469, 5548* (SAT); *JF 1038, OCW 337* (SRSC).

§ *Dalea jamesii* (Torr.) Torr. & A. Gray, James prairie clover, perennial herb; *BA2 5228* (SAT).

§ *Dalea laniceps* Barnebey, Woolyhead prairie clover, perennial herb; *MT 150* (SRSC).

§ *Dalea leporina* (Aiton) Bullock, Foxtail prairie clover, annual herb, DSC; *OCW 584-21* (TAES).

§ *Dalea longipila* (Rydb.) Cory, Downy prairie clover, uncommon perennial herb, DSC, DAR, ca. 2500 ft; *AMP & SAP 6140, BLT & MT2 97-344* (SRSC); *BLT & MT2 97-344* (TEX-LL).

+ *Dalea nana* Torr. & A. Gray, Dwarf prairie clover, uncommon perennial herb, DAR, SYG/CHP, 2750–5700 ft; *JF 959, 1265* (SRSC).

Dalea neomexicana (A. Gray) Cory, New mexico dalea, "frequent" perennial herb, DSC, DCA, 1800–3440 ft; *BHW 13032* (BIBE); *JF 357, BHW 13032, BHW & MCJ 16679, BHW & BLT 8319, GLW 4473* (SRSC); *BHW 13030* (TAES); *BLT & MT2 97-334, BHW 13032, BHW & BLT 8319* (TEX-LL).

Dalea pogonathera A. Gray var. *pogonathera*, Bearded dalea, uncommon perennial herb, DSC, DAR, 3560 ft; *BRM 3119, OCW 5094* (BGWMA); *JF 461* (BIBE & SRSC); *BHW & LCH BG-196* (SRSC); *BA2 5377, 5488* (SAT); *VLC 43968* (TEX-LL).

§ *Dalea terminalis* M.E. Jones, [*Dalea lanata* var. *terminalis* (M.E. Jones) Barneby], Wooly prairie clover, uncommon perennial herb, DSC, DCA, 1800 ft; *BA2, DG, TE, & PC 4602, BHW 13030* (BIBE); *BLT, JDA & BHW 8337, BHW 13030, GLW 4480* (SRSC); *BHW 13030* (TAES); *DSC & HBC 30629, BHW 13030* (TEX-LL).

Dalea wrightii A. Gray, Wright dalea, uncommon perennial herb, DSC, DAR, 2750–3560 ft; *BA2 5430* (SAT); *JF 282, 468a, 962, MT 13, 15, 220, BLT & MT2 97-345, 97-349, BHW C300* (SRSC); *VLC 43969, BHW C300* (TEX-LL).

Desmanthus velutinus Scheele, Velvet bundleflower, uncommon perennial herb, DSC, DAR, SYG, 3360–5840 ft; *JF 227, 322, 713a, 1097, 1910, 1978, MT 35* (SRSC).

Eysenhardtia texana Scheele, Texas kidneywood, occasional shrub, DCA, DAR, 1800–4150 ft; *WFM 27, CMR 5125, 11611, OCW s.n., 320a* (BGWMA); *BA2 5254* (SAT); *SCB 223, JF 201, 1112, 1929, 2136, JF & MY 1318, MT 195, OCW 320, BHW & LCH BG-63* (SRSC).

Galactia sp., Milkpea, rare perennial herb, DAR, DCA, 1800–2780 ft; *JF 961* (BIBE); *JF 188, 940, 961, 1060, 2090, 2141* (SRSC); *JF 2090* (TEX-LL).

+ *Hoffmannseggia drepanocarpa* A. Gray, Sicklepod rushpea, rare annual herb, SYG, 5300 ft; *JF 1998* (SRSC).

Leucaena retusa Benth., Goldenball leadtree, woohoo tree, occasional tree, DSC, DAR, DCA, 2200–5200 ft; *WFM s.n.* (BGWMA); *PVW s.n.* (KANU); *BA2 5190* (SAT); *JF 748, 1020, 1309, AMP & SAP 5144, TR 19, OCW 1, BHW 10849, BHW & LCH BG-135, GLW 4472* (SRSC); *RB 1502, BHW & LCH BG-135* (TEX-LL).

§ *Lupinus havardii* S. Watson, Big bend bluebonnet, annual herb, DAR, 2560 ft; *OES 1344* (TEX-LL).

*§● *Medicago sativa* L., Alfalfa, annual herb, 1800 ft; *EGM 136a* (BIBE & SRSC).

*§ *Melilotus indicus* (L.) All., Annual yellow sweetclover, "infrequent" annual herb, 1800 ft; *HTF 1225* (SRSC).

Mimosa aculeaticarpa Ortega var. *biuncifera* (Benth.) Barneby, Catclaw mimosa, common shrub, DSC, DAR, DCA, 3050 ft; *WFM 26, 29, 30* (BGWMA); *BA2 5238, 5702* (SAT); *JF 1150* (SRSC).

Mimosa borealis A. Gray, Fragrant mimosa, "infrequent" to common shrub, DAR, DCA, 1900–3760 ft; *JF 711, 1693, BHW 21186* (SRSC).

Mimosa emoryana Benth., Emory mimosa, occasional shrub, DSC, DAR, DCA, 2850–3560 ft; *JF 848, 970, GLW 4445* (SRSC).

+ *Mimosa texana* (A. Gray) Small, Catclaw, occasional shrub, DAR, DCA, SYG, 1800–4600 ft; *JF 1015, 1019, 1357, 2145* (SRSC).

Mimosa turneri Barneby, Desert mimosa, Turner mimosa, uncommon shrub, DSC, DAR, SYG, 3000–4900 ft; *JF 1161, 1467, 1552, 2188* (SRSC).

Parkinsonia aculeata L., Retama, Jerusalem thorn, rare tree, RIO, 1800 ft; *DG 217* (BIBE); *JF 2257* (SRSC).

Peteria scoparia A. Gray, Rush peteria, rare shrub, DSC, 3840 ft; *JF 247* (SRSC).

Pomaria melanosticta S. Schauer [*Caesalpinia parryi* (E. Fisher) Eifert, Correll & Johnston; *Caesalpinia melanosticta* (S. Schauer) Fisher; *Caesalpinia wootonii* (Britt.) Eifert ex Isely; *Hoffmannseggia parryi* (Fisher) B.L. Turner], Parry holdback, occasional subshrub, DSC, DAR, DCA, 1800–3500 ft; *BRM 3148, CMR 5143a-c, BHW & LCH s.n.* (BGWMA); *AL 183; BHW 884, 12891* (BIBE); *BA2 5383, 5431* (SAT); *JF 148, 343, 655, 1328, 2130, 2182, BLT & MT2 97-332, BHW 10830, 12891, 20952, BHW & LCH BG-141, BHW & MCJ 16063, 16835, MT 221* (SRSC); *BHW & MCJ 16835* (SWT); *BLT & BD 23-168, BLT & MT2 97-332, BHW 12891, BHW & LCH BG-141* (TEX-LL).

+ *Prosopis glandulosa* Torr. var. *torreyana* (L. D. Benson) M.C. Johnst., Mesquite, occasional shrub or tree, DSC, DAR, SYG, 1800–4400 ft; *JF 807* (SRSC).

+ *Rhynchosia senna* Gillies ex Hook. & Arn. var. *texana* (Torr. & A. Gray) M.C. Johnst., Texas snoutbean, rare perennial herbaceous vine, DCA, 3050 ft; *JF 1119* (BIBE & SRSC).

+ *Senna bauhinioides* (A. Gray) H.S. Irwin & Barneby, Twinleaf senna, occasional perennial herb, DSC, 2400–3000 ft; *JF 1457, 1465* (SRSC).

Senna lindheimeriana (Scheele ex Schltdl.) H.S. Irwin & Barneby, Lindheimer sennna, rare perennial herb, DSC, DAR, 1800 ft; *JF 2072, MT 101* (SRSC).

Senna orcuttii (Britton & Rose) H.S. Irwin & Barneby, Orcutt senna, uncommon (G2S2) perennial herb, SYG, CHP, 4200–5250 ft; *JF 1030* (BIBE); *JF 827, 1030, 1218, 1244, 2191, MT 110, BLT 22-153* (SRSC); *JF 1030, BLT 22-153* (TEX-LL).

Senna pilosior (Robinson ex J. F. Macbr.) H.S. Irwin & Barneby [*Senna durangensis* (Rose) H.S. Irwin & Barneby], Trans-Pecos senna, occasional perennial herb, DSC, DCA, 1800–3500 ft; *JF 437, 673, 1326, 1603, 2020, 2048, CN T263, BHW 20953, GLW 4475* (SRSC); *LEB 9640* (TAES); *BHW 20727* (TEX-LL).

§ *Senna pumilio* (A. Gray) H.S. Irwin & Barneby, Dwarf senna, 3200 ft; *PDW & BHW 319* (SRSC).

Senna ripleyana (H.S. Irwin & Barneby) H.S. Irwin & Barneby, Ripley senna, rare (G1SH) perennial herb, SYG, 4320–5000 ft; *JF 820, 1518, MT 214* (SRSC).

§ *Sophora secundiflora* (Gomez-Ortega) Lag. ex DC., Mescal bean, shrub, DCA; *BRM 3248* (BGWMA).

Vicia ludoviciana Nutt. var. *occidentalis* (Shinners) B.L. Turner,

Deer pea vetch, uncommon annual herb, DCA, 3560 ft; *BRM 3114* (BGWMA); *JF 540, BHW & MCJ 15994* (SRSC).

Fagaceae

Quercus grisea Liebm., Gray oak, uncommon shrub, CHP, 4880–5680 ft; *JF 757* (BIBE); *JF 744c, 757, 1246, 1258, 1280, 1282, 1320, MT 149, 225, 240, 250* (SRSC); *JF 1282* (TEX-LL).

§ *Quercus intricata* Trel., Dwarf oak, shrub, 5800 ft; *PVW s.n.* (KANU).

Quercus laceyi Small, Lacey oak, rare shrub, DCA, 4350 ft; *JF 1935* (SRSC). In Sue Peaks canyon.

Quercus mohriana Buckl. ex Rydb., Mohr shin-oak, uncommon shrub, CHP, 5240–5840 ft; *JF 1245, 1972, 2161* (SRSC).

Quercus pungens Liebm., [*Quercus pungens* subsp. *vaseyana* (Buckley) E. Murray], Sandpaper oak, occasional shrub, DSC, DCA, SYG/CHP, 3150–5680 ft; *CMR 15828, BHW & LCH s.n.* (BGWMA); *JF 303, 1223* (BIBE); *PVW s.n.* (KANU); *BA2 5193, 5203, 5214, 5224, 5225, 5243, 5251, 5275, 5279, 5328, 5450, 5459, 5485, 5709* (SAT); *JF 234, 303, 725, 736a, 749a-b, 818, 819, 1209a, 1220, 1022, 1045, 1223, 1308, 1550, 1709, 1897, JF & MY 1318a, AMP & SAP 5139, MT 76, 82, 83, 111, 112, 113, 117, 118, 130, 135, 139, 140, 142, 143, 186, 192, 194, 247, BHW 10755, 21184, 23397, BHW & LCH BG-163* (SRSC); *BHW 10755, BHW & LCH BG-163* (TEX-LL).

Fouquieriaceae

Fouquieria splendens Engelm., Ocotillo, devil's coachwhip, common shrub, DSC, SYG, 1800–4880 ft; *JM 89* (SAT); *JF 750, 779* (SRSC).

Garryaceae

Garrya ovata Benth. subsp. *goldmanii* (Wooton & Standl.) Dahling, Goldman or eggleaf silktassel, uncommon shrub, DCA, SYG, CHP, 4040–5840 ft; *PVW s.n.* (KANU); *JF 504, 770, 1202, 1239, 1307, PM 975, MT 114* (SRSC).

Gentianaceae

Centaurium arizonicum (A. Gray) A. Heller, Arizona centaury, Rosita, uncommon annual herb, DSC, DAR, RIO, 1800–3640 ft; *JF 710a, HTF 1232, MT 10* (SRSC).

Centaurium calycosum (Buckley) Fernald, Centaury, uncommon to "rare" or "sparse" annual herb, CHP, 5150 ft; *BA2 5194, 5689* (SAT); *JF 1323, AMP & SAP 5130, TR 153, MT 178, 196, BHW & LCH BG-156* (SRSC).

Eustoma exaltatum (L.) Salisb. ex G. Don, Catchfly prairie gentian, uncommon annual herb, RIO, 1800 ft; *BA2, DG, TE, & PC 4604, EGM 135, BHW 648, 13048* (BIBE); *JF 2254, BHW 13048* (SRSC); *BHW 13048* (TEX-LL).

Hydrangaceae

Fendlera falcata Thornber, Cliff fendlerbush, rare shrub, SYG, CHP, 4040–5840 ft; *JF 721a, 1266, 1277, 1963* (SRSC).

Philadelphus microphyllus A. Gray var. *microphyllus*, Littleleaf mockorange, rare shrub, SYG, CHP, 4040–4900 ft; *JF 719, 726, 753* (SRSC).

Hydrophyllaceae

#♦ *Nama dichotomum* (Ruiz & Pav.) Choisy, Wishbone fiddleleaf, rare annual herb, CHP, 5840 ft; *JF 1965* (SRSC).

Nama havardii A. Gray, Havard fiddleleaf, uncommon annual herb, DSC, DAR, 1800–3480 ft; *JF 317, 2035* (SRSC); *AT 2241* (TEX-LL).

Nama hispidum A. Gray, Bristly nama, uncommon annual herb, DSC, DAR, 1850–3560 ft; *AL 176* (BIBE); *JF 477, 1006, GLW 4467* (SRSC); *BHW C307* (TEX-LL).

Phacelia congesta Hook., Spike phacelia, bluecurls, uncommon annual herb, DAR, DCA, SYG, 2560–5080 ft; *JF 423, 505a, 744a* (SRSC); *RRI 556* (TEX-LL).

Phacelia pallida I.M. Johnst., [*Phacelia petiolata* I.M. Johnst.], Pale phacelia, rare (G2S1) perennial herb, DCA, 2780–2850 ft; *JF 185, 954* (SRSC).

§ *Phacelia popei* Torr. & A. Gray, Pope phacelia, annual herb, DCA, 2560 ft; *RRI 553* (TEX-LL).

Phacelia robusta (J.F. Macbr.) I.M. Johnst., Stout phacelia, rare to "infrequent" annual herb, DAR, DCA, 2000–3150 ft; *JF 1587, 1703, BHW 18402* (SRSC).

Juglandaceae

§ *Juglans major* (Torr.) A. Heller, Arizona walnut, tree, DCA; *CMR 2602, 2607* (SAT).

Juglans microcarpa Berland., Little walnut, occasional tree, DCA, 3050 ft; *JF 1151* (BIBE & SRSC); *WFM s.n., CMR 5130* (BGWMA); *BA2 5235* (SAT).

Krameriaceae

Krameria erecta Willd. ex Schult., Range ratany, uncommon shrub, DSC, SYG, 3800–4360 ft; *BA2 5344* (SAT); *JF 569, BHW 10792* (SRSC); *BHW 10792* (TEX-LL).

Krameria grayi Rose & Painter, White ratany, occasional shrub, DSC, DCA, RIO, SYG; 1800–4800 ft; *SMU 49, TR 52* (BGWMA); *BA2, DG, TE, & B 4920* (BIBE); *BA2 5189, 5480* (SAT); *JF 236, 371, 828, 1056, 1188, 1898, 2102, TR 17, 152, MT 85, BHW & LCH BG-195, BHW & MCJ 16863* (SRSC); *BHW 636* (TEX-LL).

Lamiaceae

Hedeoma costata Hemsl., Ribbed false pennyroyal, rare perennial herb, DCA, SYG/CHP, 4650–5680 ft; *JF 1283a, 1951* (SRSC).

§ *Hedeoma drummondii* Benth., Drummond pennyroyal, annual or perennial herb; *BLT 22-147* (TEX-LL).

Hedeoma nana (Torr.) Briq., Dwarf false pennyroyal, occasional annual or perennial herb, 2120–5800 ft; *JF 679* (BIBE); *JF 494, 534, 546, 679, 869, 949, 1042, 1270, 1329, 1702, 1719, BLT 22-152* (SRSC).

§● *Hedeoma plicata* Torr., Veiny false pennyroyal, perennial herb; *BRM 3129, CMR 5071* (BGWMA); *BLT 22-152* (TEX-LL).

#♦ *Hedeoma serpyllifolia* Small, Reverchon false pennyroyal, occasional perennial herb, DSC, SYG, 3560–5080 ft; *JF 740* (BIBE); *JF 230, 281, 740, 834* (SRSC).

§ *Mentha arvensis* L., Wild mint, rare perennial herb, 1800 ft; *EGM 158, 167, BHW 832* (BIBE); *BHW 832* (SRSC & TEX-LL).

Salvia greggii A. Gray, Autumn sage, uncommon shrub, DAR, DCA, SYG/CHP, 3500–5680 ft; *BRM & BPM 3103* (BGWMA); *JF 505, 766, 1283, 2171, TR 154, MT 107, BHW & LCH BG-171* (SRSC).

Salvia roemeriana Scheele, Cedar sage, Roemer sage, uncommon perennial herb, DCA, SYG/CHP, 2000–5840 ft; *JF 1284, 1671, 1675, 1975, BHW 18404* (SRSC); *BHW 18404* (TEX-LL).

§ *Teucrium depressum* Small [*Teucrium cubense* var. *densum* Jeps.; *Teucrium cubense* subsp. *depressum* (Small) E.M. McClint. & Epling], Small coastal germander, uncom-

mon annual herb, 1800–3520 ft; *HTF 1234, BHW 8331, GLW 4465* (SRSC).

Linaceae

Linum berlandieri Hook., Berlandier flax, occasional annual or perennial herb, DSC, DAR, DCA, SYG, 3560–4600 ft; *CMR 5090; BHW & LCH s.n.* (BGWMA); *ACK 827* (BIBE); *BA2 5338, 5568* (SAT); *JF 265, 295, 525, 552, 826, 1049, AMP & SAP 5137, BHW & LCH BG-149* (SRSC).

Linum hudsonioides Planch., Texas flax, rare perennial herb, DSC, 3800 ft; *JF & HL 1893* (SRSC).

Linum rupestre (A. Gray) Engelm. ex A. Gray, Rock flax, occasional perennial herb, DSC, DAR, DCA, 1800–3840 ft; *BRM 3136, BHW & LCH s.n.* (BGWMA); *BA2 5218, 5310, 5703* (SAT); *JF 241, 276, 847, 1016, 2071, MT 48, 177, TR 282, OCW 509, BHW 10828, BHW & LCH BG-84, BG-164* (SRSC); *BHW 10828* (TEX-LL).

Loasaceae

Cevallia sinuata Lag., Stinging cevallia, occasional perennial herb, DSC, DAR, DCA, 2000–3400 ft; *CMR 5077* (BGWMA); *JF 172, 808, 1383, 1724, MT 218* (SRSC).

Eucnide bartonioides Zucc., Yellow rocknettle, uncommon to occasional annual or perennial herb, DSC, DCA, 1800–3700 ft; *BA2 & PC 4754* (BIBE); *BRM 3104* (BGWMA); *BA2 4754, 5509* (SAT); *JF 177, 286, 532, 2089, BHW 18400, 20619* (SRSC).

+o *Mentzelia mexicana* H.J. Thompson & Zavortink, Mexican blazingstar, rare perennial herb, DAR, DCA, 1800 ft; *JF 2031, 2066* (SRSC).

+Δo *Mentzelia multiflora* (Nutt.) A. Gray, Desert mentzelia, annual or perennial herb, observed at the Boquillas restoration site.

+o *Mentzelia oligosperma* Nutt., Chickenthief, stickleaf, rare perennial herb, DSC, DCA, 2350–3720 ft; *JF 231, 1333* (SRSC).

Mentzelia pachyrhiza I.M. Johnst., Coahuila blazingstar, uncommon perennial herb, DSC, DCA, 2850–3640 ft; *JF 312, 840, 950, BHW 13071* (SRSC).

Loganiaceae

Buddleja marrubiifolia Benth., Wooly butterflybush, occasional shrub, DSC, DAR, DCA, 1850–3900 ft; *CMR 11586* (BGWMA); *SJ 6502* (SAT); *JF 150, 436, 835, 1375, 1721, 2012, MT 9, 168, BHW 10759, BHW & LCH BG-77* (SRSC); *BHW 10759, BHW & LCH BG-77* (TEX-LL).

Lythraceae

§ *Lythrum californicum* Torr. & A. Gray, California loosestrife, "infrequent" perennial herb, 1800 ft; *BHW 896* (TEX-LL).

Malphigiaceae

Janusia gracilis A. Gray, Helicopter bush, slender janusia, occasional perennial herbaceous vine, DSC, DAR, DCA, 1800–3720 ft; *EGM 122* (BIBE); *CMR 15112* (SAT); *JF 242, 647, 1332, AMP & SAP 5308, BLT & MT2 97-377, BHW 10793* (SRSC); *BLT & MT2 97-337* (TEX-LL).

Malvaceae

Abutilon malacum S. Watson, Yellow indian mallow, uncommon subshrub, DSC, DAR, DCA, 1850–2050 ft; *EGM 154* (BIBE); *JF 643, 1082, 1604, 1643, 2004, 2019, BHW 12886* (SRSC).

Abutilon parvulum A. Gray, Dwarf indian mallow, uncommon perennial herb, DSC, DAR, DCA, 2750–3700 ft; *AF 187* (BIBE); *JF 841, 969, 1140, 2169* (SRSC).

Abutilon wrightii A. Gray, Wright indian mallow, occasional perennial herb, DSC, DAR, DCA, 1800–3560 ft; *TR s.n.* (BGWMA); *JF 469a, 668, 1011, 1648, 2084, BLT & BD 23-171* (SRSC); *BLT & BD 23-171, BHW 9158, 10839* (TEX-LL).

§ *Herissantia crispa* (L.) Brizicky, Netvein mallow, "frequent" subshrub, DSC, DAR, 1800–1900 ft; *HCH s.n., BHW 13064* (SRSC); *HCH s.n.* (TEX-LL).

Hibiscus coulteri Harv. ex A. Gray, Desert rosemallow, occasional subshrub, 2400–4300 ft; *JF 444, 846, 1480, 1582, 2184, MT 51, BHW 10820, BHW & LCH BG-152* (SRSC); *BHW 10820, BHW & LCH BG-152* (TEX-LL).

Hibiscus denudatus Benth., Paleface rosemallow, rare subshrub, DSC, DCA, 3200 ft; *BRM 3120* (BGWMA); *JF 1471* (SRSC).

§ *Hibiscus martianus* Zucc.– Heartleaf rosemallow, "sparse" subshrub, 2100 ft; *OCW 358* (SRSC).

*# <u>*Malva parviflora*</u> L., Cheeseweed mallow, rare annual or perennial herb, RIO, 1800 ft; *AL 304, 308* (BIBE & SRSC).

§● *Malvella lepidota* (A. Gray) Fryxell, Scurfymallow, perennial herb, DAR, 2560 ft; *OES 1335* (TAES).

Malvella leprosa (Ortega) Krapov., Alkali mallow, dollarweed, rare perennial herb, DSC/DAR, 2400 ft; *JF 1423* (SRSC).

§ *Rhynchosida physocalyx* (A. Gray) Fryxell, Spearleaf sida, buffpetal, "infrequent" perennial herb, 2250 ft; *BRM 3171* (BGWMA); *BHW & LCH BG-194* (SRSC).

Sida abutifolia Mill., Spreading sida, occasional perennial herb, DSC, DCA, 1800–2850 ft; *JF 166, 956, 1325, 1439, 2008, HCH s.n.* (SRSC).

+o *Sida longipes* A. Gray, Stockflower fanpetals, uncommon perennial herb, DSC, DAR, SYG, 3440–4800 ft; *JF 1539, 1920, 2175* (SRSC).

Sphaeralcea angustifolia (Cav.) G. Don, Narrowleaf globemallow, occasional perennial herb, DSC, DAR, DCA, RIO, SYG, 1800–5300 ft; *BRM 3121, CMR 11593* (BGWMA); *CN 499* (BIBE); *JF 585, 803, 1415, 1461, 1986, 2104, 2268, BH 641* (SRSC); *BHW 247* (TEX-LL).

§● *Sphaeralcea hastulata* A. Gray, Spear globemallow, "infrequent" perennial herb, DCA, 2560 ft; *RRI 21431* (TEX-LL).

Nyctaginaceae

Acleisanthes angustifolia (Torr.) R.A. Levin, Narrowleaf monopod, occasional to uncommon subshrub, DSC, DAR, DCA, 1800–3720 ft; *JF 243* (BIBE); *JF 243, 844, 1352, 2015, 2022, BLT & BD 23-160, BHW 9159, 10790, BHW & MCJ 16846, BHW & BLT 8324* (SRSC); *BLT & BD 23-160, BLT & MT2 97-346b, BHW 10790* (TEX-LL).

Acleisanthes longiflora A. Gray, Angel trumpets, hierba de la rabia, uncommon perennial herb, DSC, DCA, 1850–4000 ft; *BA2 5188* (SAT); *JF 1070, MT 157, GLW 4479* (SRSC).

Allionia incarnata L. var. *incarnata*, Trailing four o'clock, pink windmills, occasional perennial herb, DSC, DCA, 1800–2750 ft; *EGM 168* (BIBE); *BA2 5356* (SAT); *JF 171, 651, 936, 2065, AMP & SAP 5304, BHW 20879, BHW & MCJ 16848* (SRSC); *BHW 702* (TEX-LL).

§ *Ammocodon chenopodioides* (A. Gray) Standl. [*Acleisanthes chenopodioides* (A. Gray) R.A. Levin], Goosefoot monopod, perennial herb; *BLT & BD 23-160* (SRSC).

§ *Anulocaulis eriosolenus* (A. Gray) Standl. [*Boerhavia eriosolena* A. Gray], Big bend ringstem, "infrequent to locally common" annual or perennial herb, DSC, DAR, DCA, 1800–2320 ft; *EGM 146* (BIBE); *AMP & SAP 6141, BLT & MT2 97-351, BHW 16676, 20878, 20949* (SRSC); *DSC & HBC 30639, OES 1632, BLT & MT2 97-340* (TEX-LL).

Boerhavia anisophylla Torr., Wineflower, uncommon perennial herb, DAR, DCA, 1800–3000 ft; *JF 1468, 2073, 2134, AMP & SAP 3614, BHW 16690, BHW, BLT, & JDA 8335* (SRSC); *BHW 21031, BHW, BLT, & JDA 8335* (TEX-LL).

+ *Boerhavia coccinea* Miller, Red spiderling, rare annual or perennial herb, DCA, 3065 ft; *JF 1120* (SRSC).

§ *Boerhavia intermedia* M.E. Jones, Spreading spiderling, uncommon to "frequent" annual herb, DSC, DAR, DCA, 1800–2320 ft; *AMP, SAP, MLP & AL2 6102, TRV s.n., BHW 20877, BHW & LCH BG-185BHW & BLT 8315* (SRSC); *HCH s.n., AMP & SAP 3614, BLT & MT2 97-342* (TEX-LL).

§ *Boerhavia linearifolia* A. Gray, Narrowleaf spiderling, annual herb, 4600 ft; *BA2 6190, CMR 5060, OCW 5810-1* (BGWMA); *BA2 5326* (SAT); *AMP & SAP 5120* (SRSC).

§ *Boerhavia spicata* Choisy, Creeping spiderling, "infrequent to frequent" annual herb, 1800 ft; *BHW 695, 20948, BHW & MCJ 16849* (SRSC).

§ *Boerhavia torreyana* (S. Watson) Standl., Creeping spiderling, annual herb, 2100 ft; *BHW 8315* (TEX-LL). Head of Boquillas Canyon in 1948. A newer taxon recognized in the Flora.

Cyphomeris gypsophiloides (M. Martens & Galeotti) Standl., Birdfruit, red cyphomeris, uncommon perennial herb, DSC, DAR, DCA, SYG, 1800–4360 ft; *JF 348* (BIBE); *BA2 5449* (SAT); *JF 348, 545, 951, 1172, 2086* (SRSC).

§ *Mirabilis albida* (Walter) Heimerl, White four o'clock, perennial herb; *BA2 5527* (SAT).

Mirabilis linearis (Pursh) Heimerl, Linearleaf spiderling, rare perennial herb, SYG/CHP, 5300–5840 ft; *JF 1982, 2159* (SRSC).

Mirabilis texensis (J.M. Coult.) B.L. Turner, Texas mirabilis, uncommon perennial herb, DSC, DAR, DCA, 2750–4200 ft; *JF 165, 809, 960, 1502, 2173, BLT & MT2 97-343, BHW 10776, 10844, BHW & MCJ 16829* (SRSC); *BLT & MT2 97-343* (TEX-LL).

§ *Nyctaginia capitata* Choisy, Devil's boquet, perennial herb; *TM 137* (SAT).

Oleaceae

Forestiera angustifolia Torr., Narrowleaf forestiera, common shrub, DSC, DAR, DCA, 1920–4400 ft; *BHW & LCH BG-153* (BGWMA); *BA2 5256, 5266* (SAT); *JF 374, 493, 572a, 2181, JF & HL 1899, AMP & SAP 5826, BHW 18411, 21203, BHW & LCH BG-153, BHW & MCJ 15996, GLW 4459* (SRSC); *WBM 2022* (TAES).

Fraxinus cuspidata Torr., Fragrant ash, rare to "sparse" tree, DAR/DCA, 3500–4800 ft; *BHW & LCH BG-173* (BGWMA & SRSC); *JF 1947* (SRSC).

Fraxinus greggii A. Gray, Gregg ash, common shrub, DSC, DAR, DCA, SYG, 2500–4900 ft; *TR 243* (BGWMA); *BA2 5358, 5570* (SAT); *JF 246, 568, 728, 1131, TR 296, MT 07b, BHW 20623, BHW & MCJ 15983* (SRSC).

Menodora longiflora A. Gray, Showy menodora, twinpod, occasional perennial herb, DSC, DAR, DCA, 2350–4600 ft; *CMR 5062, OCW 9027* (BGWMA); *JF 334* (BIBE); *BA2 5447, 5528* (SAT); *JF 226, 334, 517, 946, 1115, 1359, 1360, AMP & SAP 5122, 5145, MT 7* (SRSC).

Menodora scabra A. Gray, Rough menodora, common subshrub, DSC, DAR, DCA, 1800–5080 ft; *BHW 1123, 12887* (BIBE); *BA2 5699* (SAT); *JF 582, 754, 1482, 1520, BGH 639, MT 56, 180, 222, BHW 10783, 10803, 12887, 13037* (SRSC); *BHW 10783, 12887* (TEX-LL).

Onagraceae

§ *Calylophus greggii* A. Gray [*Calylophus hartwegii* (Benth.) P.H. Raven subsp. *pubescens* (A. Gray) Towner & P.H. Raven], Gregg sundrops, "infrequent" subshrub, 2150 ft; *HTF 1225* (SRSC).

Calylophus hartwegii (Benth.) P.H. Raven subsp. *hartwegii*, Hartweg sundrops, uncommon perennial herb, DCA, 1800–3050 ft; *BA2, DG, TE, & PC 4609* (BIBE); *BA2 5247* (SAT); *JF 1110, 117a, OCW 508* (SRSC).

Gaura boquillensis P.H. Raven & D.P. Gregory, Boquillas gaura, occasional (G2S2) subshrub, DSC, DCA, RIO, 1800–4400 ft; *JS & AL 301, 304* (BIBE); *JF 1363, 1380, 1538, 2091, 2117, 2147, AMP & SAP 3608, BHW 1008, 18397, GLW 4481* (SRSC); *BHW 1008* (TAES); *AMP & SAP 3608* (TEX-LL).

§ *Gaura calcicola* P.H. Raven & D.P. Gregory, Texas beeblossom, "infrequent" perennial herb; 2200–2400 ft; *TR 75* (SRSC).

Gaura coccinea Pursh, Scarlet gaura, occasional perennial herb, DSC, DAR, 2200–3520 ft; *TR 75* (BGWMA); *BA2 5186, 5248, 5290, 5306, 5522, 5563, 5576* (SAT); *JF 1418, 1460, BLT & BD 23-173, GLW 4449* (SRSC); *BLT & BD 23-173* (TEX-LL).

§ *Gaura parviflora* Lehm. [*Gaura mollis* Kunth], Velvetweed, perennial herb, RIO, 1800 ft; *AL 305* (BIBE).

§ *Ludwigia peploides* (Kunth) P.H. Raven, Floating primrose-willow, "infrequent to rare" perennial herb; RIO, 1800 ft; *HTF 1231, EGM 159* (SRSC); *EGM 159, BHW C297* (TEX-LL).

+ *Oenothera brachycarpa* A. Gray, Shortpod evening-primrose, rare perennial herb, DCA, SYG/CHP, 3560–5200 ft; *JF 521, 1311, 1953* (SRSC).

Oenothera kunthiana (Spach) Munz, Kunth sundrops, occasional annual or perennial herb, DSC, DAR, DCA, RIO, 1800–3560 ft; *BRM 3170, CMR 5139* (BGWMA); *JF 510, HTF 1229, AMP & SAP 4300, 5388, BHW 18384, 47055* (SRSC); *RRI & BHW 21362* (TEX-LL).

§● *Oenothera laciniata* Hill, Cutleaf evening-primrose, annual or perennial herb; *BA2 5513, 5574* (SAT).

§ *Oenothera primiveris* A. Gray, Large yellow desert primrose, "frequent" annual herb, 2000 ft; *BHW & MCJ 16088* (SRSC & TEX-LL).

+ <u>*Oenothera rosea*</u> L'Hér. ex Aiton, Rose sundrops, rare perennial herb, DCA, 1800–3000 ft; *JF 798, 2076* (SRSC).

§ *Oenothera triloba* Nutt., Stemless evening-primrose, "infrequent" annual or biennial herb, 1800–4000 ft; *BA2 5564* (SAT); *HTF 1228* (SRSC).

Orbanchaceae

Orobanche ludoviciana Nutt., Louisiana broomrape, uncommon annual herb, DAR, DCA, 1800–2120 ft; *BRM 3172* (BGWMA); *JF 677* (SRSC); *DSC & WOD 30714, BHW 838* (TEX-LL).

Orobanche multicaulis Brandegee, Spiked broomrape, oc-

casional annual herb, DAR, DCA, RIO, 1800–4080 ft; *JF 564, 931, BHW 738* (SRSC).

Oxalidaceae

§ *Oxalis drummondii* A. Gray, Drummond woodsorrel, perennial herb; *MT 228* (SRSC).

Papaveraceae

+ *Argemone chisosensis* G.B. Ownbey, Chisos mountain pricklepoppy, rare annual or perennial herb, DSC, DAR, 2350–2400 ft; *JF 1414, 1579* (SRSC).

§ *Argemone mexicana* L., Mexican pricklepoppy, rare annual herb, RIO, 1800 ft; *AL 299* (BIBE); *AL 300* (SRSC).

Argemone sanguinea Greene, Red pricklypoppy, rare annual or perennial herb, DSC/DAR, DCA, 2800 ft; *CMR 2605* (SAT); *JF 966* (SRSC).

Passifloraceae

Passiflora tenuiloba Engelm., Passionflower vine, occasional perennial herbaceous vine, DSC, DAR, DCA, 1800–4280 ft; *BRM 3150, 3150b; CMR 5082* (BGWMA); *AL 142, 143, 318* (BIBE); *BA2 5215* (SAT); *JF 189, 306, 963, 1076, 1361, 1591, 2129, TR 281, BHW 20606* (SRSC); *TR 249* (TEX-LL).

Pedaliaceae

§ *Proboscidea louisianica* Thell. subsp. *fragrans* (Lindl.) Bretting, Devil's claw, "infrequent" annual herb; 1800 ft; *BHW 12890* (SRSC).

Phytolaccaceae

Rivinia humilis L., Pigeonberry, uncommon perennial herb, DAR, DCA, 2920–3050 ft; *CMR 5031* (BGWMA); *JF 216a, 1137* (SRSC).

Plantaginaceae

Plantago helleri Small, Heller plantain, locally common annual herb, DSC, SYG/CHP, 3300–5300 ft; *OCW 584-20* (BGWMA); *JF 620, 785, 1250* (SRSC).

§ *Plantago hookeriana* Fisch. & C.A. Mey., California plantain, "infrequent" annual herb, DCA, 2560 ft; *BHW 21422* (TEX-LL).

+○ *Plantago patagonica* Jacq., Bristlebract plantain, uncommon annual herb, DSC, DAR, DCA, SYG, 1800–5300 ft; *JF 1252, 1609, 2082* (SRSC).

Plantago rhodosperma Decne., Redseed plantain, uncommon annual herb, DSC, DAR, DCA, 2350–2560 ft; *BRM 3112* (BGWMA); *RH 20, 43* (SAT); *JF 1335, 1430* (SRSC); *RRI 21423* (TEX-LL).

Polemoniaceae

Gilia incisa Benth., Splitleaf gilia, rare annual or perennial herb, DSC, 2850–4000 ft; *BA2 5308, 5573, 5577* (SAT); *JF 944* (SRSC).

§ *Gilia insignis* (Brand) Cory & H.B. Parks, Marked gilia, "infrequent" perennial herb, 2250 ft; *BHW & LCH BG-200* (SRSC).

Gilia rigidula Benth. subsp. *acerosa* (A. Gray) Wherry, Button gilia, blue gilia, uncommon annual herb, DSC, 3560–4300 ft; *BA2 5372* (SAT); *JF 245, 284, 870, MT 97* (SRSC).

Gilia stewartii I.M. Johnst., Stewart gilia, uncommon annual herb, DSC, DAR, 3400–4800 ft; *BRM 3221* (BGWMA); *BA2 5557* (SAT); *JF 498, 814, 1026, 2163, BHW 10761* (SRSC); BHW 10761 (TEX-LL).

§ *Ipomopsis havardii* (A. Gray) V.E. Grant, Havard ipomopsis, "infrequent" perennial herb; *BHW & MCJ 15907* (SRSC).

§● *Phlox nana* Nutt., Santa Fe phlox, [*Phlox mesoleuca* Greene], perennial herb; *BA2 5371, 5519, 5562* (SAT).

Polygalaceae

Polygala alba Nutt., White milkwort, uncommon perennial herb, DSC, CHP, 3500–5150 ft; *ACK 828* (BIBE); *BA2 5212, 5378* (SAT); *JF 251, 1227, MT 72, BHW & LCH BG-158* (SRSC).

Polygala barbeyana Chodat, [*Polygala longa* S.F. Blake], Narrowleaf polygala, occasional to uncommon perennial herb, DSC, DAR, DCA, SYG, 2200–5500 ft; *TR 122, BHW & LCH s.n.* (BGWMA); *BHW 1006* (BIBE); *BA2 5286, SJ 6506* (SAT); *JF 158, 252, 267, 288, 864, 1099, 1160, 1259, 1503, 2174, 2183, TR 122, CMR 5070, MT 28, 244, BHW 10798, 21197, 23401, BHW & LCH BG-169, BHW & MCJ 16826* (SRSC); *BLT & BD 23-172b, BHW 10798* (TEX-LL).

Polygala lindheimeri A. Gray var. *lindheimeri*, Shrubby milkwort, occasional perennial herb, DCA, 1800–3050 ft; *BA2 5196, 5244, 5696* (SAT); *JF 964, 1009, 1058, 1071, 1148, 2070, MT 12, 29, 200, BHW 10809, BHW & LCH BG-70, BG-134, BG-182* (SRSC); *JF 1071, BHW & LCH BG-134* (TEX-LL). This may be the species' western limit according to Turner et al. (2003). These two varieties intergrade in Brewster and Presidio County, and some individuals demonstrate mixed characters [e.g., *JF 964* (SRSC); Powell in prep.].

+ *Polygala lindheimeri* A. Gray var. *parvifolia* Wheelock [*Polygala tweedyi* Britton ex Wheelock], Shrubby milkwort, uncommon perennial herb, DSC, DCA, 1850–2600 ft; *JF 929, 1081* (SRSC).

Polygala macradenia A. Gray, Glandleaf milkwort, common perennial herb, DSC, DAR, DCA, 1850–4360 ft; *BRM 3226* (BGWMA); *ACK 824* (BIBE); *BA2 5228, 5547, 5553* (SAT); *JF 239, 275, 354, 854, 1529, 2007, BHW 10797, 20955, BHw & BLT 8316, GLW 4446* (SRSC); *BLT & BD 23-166, TRV, GLB & WEH 85-46, BHW & BLT 8316* (TEX-LL).

Polygala nudata Brandegee, Littleleaf milkwort, rare perennial herb, DSC, DCA, 1800–>4000 ft; *BA2, DG, TE, & B 4932, AL 312* (BIBE); *JF 1670, 1698, 2126* (SRSC).

Polygala scoparioides Chodat, Broom milkwort, occasional perennial herb, DSC, DAR, DCA, 2200–4800 ft; *CMR 5064, 11590* (BGWMA); *BA2 5289, SJ 6499* (SAT); *JF 425, 506, 580, 1165, 1190, 1365, TR 124, OCW 502, BHW 20624, 21199, GLW 4440, 4452* (SRSC); *BLT & BD 23-165, 23-172a* (TEX-LL).

Polygonaceae

Eriogonum havardii S. Watson, Havard buckwheat, rare perennial herb, DSC, 3350 ft; *JF 1718* (BIBE & SRSC); *JF 1714* (SRSC).

Eriogonum platyphyllum Torr. ex Benth., Broad-leaf wild buckwheat, occasional perennial herb, DAR, DCA, 1950–4600 ft; *JF 939, 1381, 1635, AMP & SAP 5123* (SRSC).

+○ *Eriogonum rotundifolium* Benth., Roundleaf buckwheat, rare annual herb, DAR, 2350 ft; *JF 1384* (SRSC).

§ *Eriogonum tenellum* Torr., Tall wild buckwheat, perennial herb; *BRM 3206* (BGWMA).

§ *Polygonum hydropiperoides* Michx., Swamp smartweed, "infrequent" perennial herb, 1800 ft; *BHW, BLT & JDA 8336* (SRSC).

§ *Polygonum pensylvanicum* L., Pennsylvania smartweed, [*Persicaria pensylvanica* (L.) M. Gómez], annual herb, 1800 ft; *BHW 641* (BIBE).

*§ *Persicaria maculosa* Gray [*Polygonum persicaria* L.], Spotted ladysthumb, "infrequent" annual herb, 1800–1850 ft; *EGM 161, BHW 642* (BIBE); *BHW 21517* (TEX-LL).

*§ *Rumex crispus* L., Curly dock, "infrequent" perennial herb, 1800 ft; *BHW 18387* (SRSC).

#♦ *Rumex maritimus* L., Golden dock, rare annual or biennial herb, DCA, 1800 ft; *JF 2118* (SRSC).

Portulacaceae

Talinum angustissimum (Engelm.) Wooton & Standl [*Phemeranthus aurantiacus* (Englem.) Kiger], Narrow-leaf fameflower, rare perennial herb, DAR, 1900 ft; *JF 2040a* (SRSC). Many treatments include this species under *Phemeranthus aurantiacus*: the Flora of North America (FNA 2003a) states that the purported distinctions creating separate species break down under a continuum of intergradation, but collections examined from Brewster County (*JF 2270-2274* SRSC) demonstrate that individuals clearly representing both concepts occur at the same site with no intergradation of characters (Powell in prep.).

+ *Phemeranthus aurantiacus* (Engelm.) Kiger [*Talinum aurantiacum* Engelm.], Orange fameflower, rare perennial herb, DSC, 3880 ft; *JF 293, 2040a* (SRSC).

Phemeranthus brevicaulis (S. Watson) Kiger, Dwarf fameflower, [*Talinum brevicaule* S. Watson], rare, locally common perennial herb, SYG/CHP, 5320–5840 ft; *JF 1967, 1967a* (SRSC).

Portulaca oleracea L., Purslane, verdolaga, rare annual herb, DAR, DCA, 2500–2880 ft; *TR s.n.* (BGWMA); *JF 204* (SRSC).

Portulaca pilosa L., Kiss me quick, occasional annual or perennial herb, DSC, DAR, DCA, SYG/CHP, 1800–5840 ft; *BHW 12901* (BIBE); *BA2 5281, 5379* (SAT); *JF 176, 240, 272, 1154, 1979, 2099, MT 6, 209, 243, BHW 12901, JF & MY 1316, BHW & MCJ 16843* (SRSC); *BHW 12901* (TEX-LL).

Primulaceae

§ *Anagallis arvensis* L., Scarlet pimpernel, annual or biennial herb, RIO, 1800 ft; *AL 303* (BIBE).

§ *Samolus ebracteatus* subsp. *cuneatus* (Small) R. Knuth, Limewater brookweed, "infrequent" perennial herb, RIO, 1800 ft; *EGM 130* (BIBE); *HTF 1223, BHW 13049* (SRSC).

Ranunculaceae

Anemone tuberosa var. *texana* Enquist & Crozier, Desert windflower, tuber anemone, rare perennial herb, DSC, DCA, 2560–4440 ft; *JF 562, BHW & MCJ 15986* (SRSC).

Clematis drummondii Torr. & A. Gray, Virgin's bower, old man's beard, common perennial herbaceous vine, DAR, DCA, RIO, 1800–4080 ft; *JF 178, 1334, 1424, TR 295* (SRSC).

§ *Ranunculus scleratus* L., Cursed buttercup, rare native herb; *BHW & RLU s.n.* (SRSC).

Resedaceae

+o *Oligomeris linifolia* (Vahl) J.F. Macbr., Desert spikes, occasional annual herb, DSC, RIO, 1800–2600 ft; *JF 932, 2226* (SRSC).

Rhamnaceae

Ceanothus greggii A. Gray, Desert ceanothus, uncommon shrub, DCA, SYG, 4040–5840 ft; *PVW s.n.* (KANU); *BA2 5537* (SAT); *JF 727, 746a, 771, 1211, 1275, 1976, PM 974, MT 226, 239* (SRSC).

§ *Condalia ericoides* (A. Gray) M.C. Johnst., Javelinabush, shrub; *CMR 11624* (SAT).

Condalia viridis I.M. Johnst., Green condalia, occasional shrub, DSC, DAR, DCA, SYG, 2350–4880 ft; *JF 161, 744b, 1348, 1386, 1421, TVR s.n.* (SRSC).

Condalia warnockii M.C. Johnst., Warnock condalia, uncommon shrub, DSC, DAR, DCA, SYG, 1800–4650 ft; *JF 1185, 2085, BHW 10814* (SRSC); *BHW 10814* (TEX-LL).

Karwinskia humboldtiana (Willd. ex Roem. & Schult.) Zucc., Coyotillo, locally uncommon shrub, DCA, RIO /DSC, 1800–3150 ft; *BHW 834* (BIBE, SRSC, & TEX-LL); *JF 1595, 2001, 2135* (SRSC).

Ziziphus obtusifolia (Hook. ex Torr. & A. Gray) A. Gray, Lotebush, occasional shrub, DSC, DAR, DCA, 2200– ca. 4000 ft; *BA2 5226, 5261, 5706* (SAT); *JF 1312, 1419, 1426, TR 117* (SRSC); *AG 380* (TEX-LL).

Rosaceae

Cercocarpus breviflorus A. Gray [*Cercocarpus montanus* Raf. var. *paucidentatus* (S. Wats) F.L. Martin], Small-leaf mountain mahogany, rare shrub, CHP, 5800–5840 ft; *PVW s.n.* (KANU); *JF 1267, 1977* (SRSC).

Cercocarpus glaberoides R.A. Denham var. *glaber* [*Cercocarpus betuloides* Nutt.; *Cercocarpus montanus* Raf. var. *glaber* (S. Wats) F.L. Martin], Smooth mountain mahogany, uncommon shrub, DCA, SYG/CHP, 3500–5680 ft; *OCW 9036, BHW & LCH s.n.* (BGWMA); *PVW s.n.* (KANU); *BA2 5439, 5452* (SAT); *JF 716, 1021, 1197, 1274, 1278, 1281, MT 64, 109, 115, OCW 338, BHW & LCH BG-150* (SRSC). Trans-Pecos mountain mahoganies were previously treated as varieties of *Cercocarpus montanus* (Powell 1998) and are now recognized by some as different species (Turner et al. 2003, Powell in prep.).

Fallugia paradoxa (D. Don) Endl. ex Torr., Apacheplume, occasional to locally common shrub, DAR, DCA, 2350–4040 ft; *BRM 3108, TR s.n.* (BGWMA); *BA2 5249, 5329* (SAT); *JF 157, 1111, 1378, PM 978, TR 114, MT 201, BHW & LCH BG-168* (SRSC); *BHW & LCH BG-88* (TEX-LL).

Malacomeles denticulata (Kunth) G.N. Jones, [*Amelanchier denticulata* (Kunth) K. Koch], Serviceberry, uncommon shrub, DCA/SYG, CHP, 3800–5080 ft; *PVW s.n.* (KANU); *BA2 5536* (SAT); *JF 511, 717, 728a, 822, 1184, 1954, BHW 10826* (SRSC); *DHR 2298, BHW 10826* (TEX-LL).

Petrophyton caespitosum (Nutt.) Rydb., Mat rockspirea, tufted rockmat, rare subshrub, SYG, 4750–5840 ft; *JF 786, 1269, MT 232* (SRSC).

Prunus havardii (W. Wight) S. C. Mason, Havard plum, uncommon to occasional shrub DAR, DCA, SYG, 3050–5840 ft; *JF 1109* (BIBE); *JF 742, 1109, 1266a, 1973, PM 973* (SRSC); *BHW & LCH BG-140* (SRSC & TEX-LL).

Purshia ericifolia (Torr. ex Gray) Henrick., Heath cliffrose, common shrub, DCA, SYG, CHP, 2050–5150 ft; *BA2 6192, CMR*

5067, 5133, 15832, TR s.n. (BGWMA); *PVW s.n.* (KANU); *BA2 5366* (SAT); *JF 751, 948, 1098, 1601, 1672, 1902, MT 25, 94, 171, TR 115, BHW 10836, 16682, 20622, BHW & LCH BG-138, BHW & MCJ 16831* (SRSC); *BHW 10836, BHW & LCH BG-138* (TEX-LL).

Vauquelinia corymbosa Humb. & Bonpl. subsp. *angustifolia* (Rydb.) W.J. Hess & Henrickson, Narrow-leaf vauquelinia, occasional shrub or tree, DCA, SYG, 4200–4800 ft; *BA2 5555* (SAT); *JF 496a, 577, 862, PM 972, BHW 10778, 10784, BHW & MCJ 16683* (SRSC); *BHW 10778* (TEX-LL).

Rubiaceae

+o *Galium proliferum* A. Gray, Limestone bedstraw, rare annual herb, DAR, DCA, SYG, 3500–5080 ft; *JF 428, 745* (SRSC).

Hedyotis acerosa A. Gray var. *acerosa*, Needleleaf bluet, common perennial herb, DSC, DAR, DCA, SYG/CHP, 3500–5840 ft; *BRM 3229* (BGWMA); *BHW 889* (BIBE); *JF 250, 287, 330, 480, 491, 824, 1051, 1101, 1717, MT 27a, 57, OCW 323, BHW 10825* (SRSC); *BHW 10825* (TEX-LL).

Hedyotis intricata Fosberg, Tangled starviolet, fascicled bluet, occasional shrub, DSC, DCA, SYG/CHP, 3800–5800 ft; *PVW s.n.* (KANU); *JF 294, 481, 749, 866, 1487, MT 91, 169, BHW & MCJ 16684* (SRSC).

Hedyotis nigricans (Lam.) Fosberg var. *nigricans*, Diamondflowers, common perennial herb, DAR, DCA, 1800–4360 ft; *BRM 3139* (BGWMA); *JF 500, AL 196* (BIBE); *BA2 5342* (SAT); *JF 156, 186, 424, 500, 541, 801, 823, 1129, 1530, 1924, 1925, 1926, 1931, JF & MY 1354* (SRSC); *BLT & MT2 97-335* (TEX-LL).

Hedyotis pooleana B.L. Turner, [*Stenaria mullerae* var. *pooleana* (B.L. Turner) Terrell], Jackie's bluet, occasional (G1T1S1) perennial herb, DSC, SYG, 2700–5680 ft; *JF 237, 713, 775, 1168, 1288, 1553, 1605, 1715, 1716, 1916, 1961, 1962, 2192, 2195, JF & MD 553, JMP 2527* (SRSC); *JMP 2527* (TEX-LL). This taxon is deserving of more systematic work; its relationship to the variable Mexican species *Houstonia mullerae*, and the regional *Hedyotis angulata* is of interest; in addition to the previously mentioned dispute over varietal versus specific designation of *Hedyotis pooleana*, two specimens of *Hedyotis angulata* seem to approach vegetative characters of *Hedyotis pooleana* (*Tharp 270, Warnock 23716* SRSC) which is supposedly restricted to the DH mountains. *Hedyotis pooleana* is also apparently slightly morphologically plastic, with a few specimens showing a more branched habit, even approaching *Hedyotis angulata*, as opposed to the characteristic densely-matted growth.

Rutaceae

Ptelea trifoliata subsp. *angustifolia* (Benth.) V.L. Bailey, Common hoptree, skunkbush, rare shrub, SYG, CHP, 4800–5680 ft; *BA2 327* (SAT); *JF 1213, 1294, 2162, MT 185* (SRSC).

Thamnosma texanum (A. Gray) Torr., Dutchman's breeches, Texas desertrue, occasional to uncommon perennial herb, DSC, DAR, DCA, SYG, 1800–5840 ft; *BRM 3122, CMR 5081* (BGWMA); *JF 488, 747, 1583, 1995, BHW 18394, BHW & LCH BG-69, BHW & MCJ 15906, GLW 4441* (SRSC).

Salicaceae

§ *Populus fremontii* S. Wats., Fremont cottonwood, locally occasional tree, RIO, 1800 ft; *EW 19709* (SRSC).

§ *Salix exigua* Nutt., Narrowleaf willow, coyote willow, "infrequent to frequent" tree; *BHW 12911* (SRSC); *BHW s.n.* (TEX-LL).

§ *Salix exilifolia* Dorn [*Salix taxifolia* Kunth], Yewleaf willow, tree; *EGM 166* (BIBE).

Salix nigra Marshall, Black willow, uncommon tree, DCA, RIO, 1800–2350 ft; *BHW 647* (BIBE); *JF 1344, BHW 18389* (SRSC); *EGM 71, BHW 21505* (TEX-LL).

Sapindaceae

+ *Sapindus saponaria* L. var. *drummondii* (Hook. & Arn.) L.D. Benson, Western soapberry, jaboncillo, rare tree, DAR, 3050 ft; *JF 1116* (SRSC).

Ungnadia speciosa Endl., Mexican buckeye, uncommon tree, DCA, 1800–4420 ft; *BRM 3109, TR 84* (BGWMA); *DB s.n.* (SAT); *JF 817, 1144, 2075, 2127, TR 84* (SRSC).

Sapotaceae

§ *Sideroxylon lanuginosum* Michx. ssp. *rigidum* (Gray) T.D. Pennington, Gum bully, ironwood, rare tree, DCA, 2560 ft; *AL 240* (BIBE); *BHW & MCJ s.n.* (SRSC).

Scrophulariaceae

§ *Castilleja integra* A. Gray var. *integra*, Wholeleaf indian paintbrush, perennial herb; *BA2 5227, 5345, 5390, 5448, 5460, 5542, 5588* (SAT); *BLT & BD 23-169* (TEX-LL).

Castilleja rigida Eastw., Rigid indian paintbrush, broadbract paintbrush, occasional perennial herb, DSC, SYG/CHP, 2150–5200 ft; *TR 111, OCW 9035* (BGWMA); *OES 1332* (BIBE); *SJ 6497* (SAT); *JF 151, 214, 331, 485, 774, 830, 833, 1210, 1580, 1720, 1908, AMP & SAP 5121, TR 111, MT 14, 126, 133, 148, 153, 154, BHW 10851, BHW & LCH BG-71* (SRSC); *BHW 10851, BHW & LCH BG-71* (TEX-LL).

Leucophyllum candidum I.M. Johnst., Boquillas silverleaf, occasional to common shrub, DSC, DAR, DCA, 1800–4080 ft; *EGM 153, BHW 13070* (BIBE); *JF 329, 567, 836, 837, 1464, 1711, 2092, 2124, PM 238, BHW 13070, BHW & LCH BG-61BHW & MCJ 16857* (SRSC); *BHW s.n.* (TEX-LL).

+ *Leucophyllum frutescens* (Berland.) I.M. Johnst., Barometer bush, ceniza, purple sage, rare shrub, DCA, 1800 ft; *JF 2083* (SRSC).

Leucophyllum minus A. Gray, Big Bend silverleaf, common shrub, DSC, DAR, DCA, 2600–4300 ft; *CMR 5066* (BGWMA); *BA 107* (BIBE); *DB s.n.* (SAT); *JF 244, 266, 470, 831, 842, 1162, MT 23, 24, 125, BLT 22-148, BHW 10804, BHW & LCH BG-161, GLW 4471* (SRSC); *BLT 22-148* (TEX-LL).

Maurandya antirrhiniflora Humb. & Bonpl. ex Willd. [*Maurandella antirrhiniflora* (Humb. & Bonpl. ex Willd.) Rothm.], Snapdragon vine, common perennial herbaceous vine, DSC, DAR, DCA, 1800–4080 ft; *BRM 3105, TR 110* (BGWMA); *JF 438, 971, TR 110, 113, MT 100, BHW 10807* (SRSC).

§ *Maurandya wislizeni* Engelm. ex A. Gray, Balloonbush, rare perennial herbaceous vine, RIO, 1800 ft; *AL 301* (BIBE); *AL 302* (SRSC).

Penstemon baccharifolius Hook., Baccharisleaf beardtongue, occasional perennial herb, DCA, 1800–4600 ft; *CMR 5061, SMU 39* (BGWMA); *AL 145* (BIBE); *JAS 3450* (NYBG); *JLB 866* (SAT); *JF 180, 838, 974, 1313, 1681, 2106, AMP & SAP 5124, TR 112, MT 95, 183, BHW & LCH BG-162* (SRSC).

Penstemon barbatus (Cav.) Roth, Beardlip penstemon, rare

perennial herb, DAR, DCA, 3160–4000 ft; *JF 222, MT 216, BHW 10732* (SRSC); *LCH & BHW BG-175* (TEX-LL).

+o *Penstemon dasyphyllus* A. Gray, Cochise beardtounge, rare perennial herb, DAR/DCA, 4120 ft; *JF 724* (SRSC).

Penstemon lanceolatus Benth., Lanceleaf beardtounge, uncommon to "rare" perennial herb, 3500–5840 ft; *JF 1306, BHW & LCH BG-175* (SRSC); *JMP 2725, BHW 10752* (TEX-LL).

Seymeria falcata B.L. Turner var. *falcata*, Falcate blacksenna, locally common annual herb, DAR/SYG, 4000–5500 ft; *JF 1943* (BIBE, BRIT, SRSC, & TEX-LL); *JF 571, 1187, 1548, 1952, 1959; MT 137* (SRSC). New to the U.S. (Fenstermacher 2006).

Seymeria scabra A. Gray, Limpia blacksenna, uncommon annual herb, SYG, 4880–5840 ft; *BA2 5330* (SAT); *JF 744d, 1302; MT 255* (SRSC).

Stemodia coahuilensis B.L. Turner, Coahuila twintip, rare annual herb, DAR, 2200 ft. Photo documented by Roy Morey in February 2007: at the first mini-side drainage encountered when walking up the wash towards Ernst Tinaja from the parking area; "one clump" of plant(s) was found. Also known from Reed Plateau (Weckesser in prep). Rare in the U.S.; mostly a Mexican species from Cuatro Cienegas area (Henrickson 2005).

Simaroubaceae

Holacantha stewartii C.H. Mull., Crucifixion thorn, rare shrub, DSC, 3480–3700 ft; *JF 1145, JF & HL 1900, BHW 11760* (SRSC).

Solanaceae

§ *Calibrachoa parviflora* (Juss.) D'Arcy, Wild petunia, annual herb, RIO, 1800 ft; *AL 309* (BIBE).

Chamaesaracha pallida Averett, Pale five eyes, false nightshade, uncommon perennial herb, DSC, DCA, SYG/CHP, 1800–4800 ft; *JF 2204, BHW 16846, 21198, BHW & MCJ 16685* (SRSC).

Chamaesaracha sordida (Dunal) A. Gray, Hairy false nightshade, occasional perennial herb, DSC, DCA, 1900–3640 ft; *BHW & LCH BG-74* (BGWMA); *JEA & MWB 519, 520, CMR 17157, TXDOT 1324* (BIBE); *JF 290, 449, 629, 654, 965, 2047, BLT & BD 23-175, BHW 20898* (SRSC); *BLT & BD 23-175* (TEX-LL).

Chamaesaracha villosa Rydb., Trans-Pecos five eyes, wooly false nightshade, uncommon perennial herb, DSC, DAR, DCA, 1900–2560 ft; *JF 1442, TXDOT s.n., BHW 21205, BHW & LCH BG-74, BHW & MCJ 15909, BHW & BLT 8327* (SRSC); *JEA & TJW 172, BHW 21205* (TEX-LL).

Datura wrightii Regel, Sacred datura, thorn apple, annual or perennial herb, RIO, 1800 ft; *JF 2262* (SRSC).

Lycium berlandieri Dunal, Berlandier wolfberry, occasional shrub, DSC, DAR, DCA, 1800–3480 ft; *EGM 10, BHW 13025* (BIBE); *JF 1090, 1387, 1390, 1391, 1451, 2045, 2110, MT 205, BHW 13025, 13067, GLW 4463* (SRSC).

+o *Lycium puberulum* A. Gray var. *berberioides* (Correll) F. Chiang, Downy wolfberry, rare shrub, DSC, 2350 ft; *JF 1392* (SRSC).

! *Nicotiana glauca* Graham, Tree tobacco, uncommon shrub, DCA, RIO, 1850 ft; *CN 11739* (BIBE); *CMR s.n.* (SAT); *JF 1063, 2260* (SRSC).

Nicotiana trigonophylla Dunal, Desert tobacco, uncommon annual herb, DSC, DAR, DCA, 2400–3500 ft; *CMR 16411* (SAT); *JF 370, 440, 1446* (SRSC).

Physalis cinerascens (Dunal) Hitchc. var. *cinerascens*, Small-flower groundcherry, uncommon perennial herb, SYG/CHP, 2300–5840 ft; *BA2 5231, 5311* (SAT); *JF 1981, MT 128, OCW 504* (SRSC).

Physalis hederifolia A. Gray, Ivyleaf groundcherry, uncommon to occasional perennial herb, DSC, DAR, DCA, 1800–4650 ft; *OES 1334* (BIBE); *JF 159, 216, 441, 1086, 1906, 2069, 2074, MT 36, 37, BHW 10779, BHW & MCJ 16825* (SRSC); *TRV & GLB 85-36, BHW 10779* (TEX-LL).

Quincula lobata (Torr.) Raf. [*Physalis lobata* Torr.], Chinese lantern, purple groundcherry, "infrequent/sparse" perennial herb, DSC, RIO, 1800–3800 ft; *BHW 1227, 10747, JF 2269* (SRSC); *BHW 10747* (TEX-LL).

Solanum elaeagnifolium Cav., Silverleaf nightshade, uncommon perennial herb, DCA, RIO, 1800–1850 ft; *EGM 160, BHW 645* (BIBE); *JF 1064* (SRSC).

§ *Solanum ptychanthum* Dunal [*Solanum americanum* Mill.], West Indian nightshade, annual herb; *EGM 137* (BIBE).

Solanum triquetrum Cav., Texas nightshade, uncommon perennial woody vine, DSC, DAR, DCA, SYG, 2780–4800 ft; *JF 162, 249a, 1035, 2176, 2178, 2185, PM 976, BHW & MCJ 16838* (SRSC).

Sterculiaceae

Ayenia filiformis S. Watson, Trans-Pecos or narrowleaf ayenia, uncommon subshrub, DSC, DCA, RIO, 1800–2250 ft; *CMR 17160* (BIBE); *JF 2034, BHW 18398, 20950, BHW & LCH BG-187* (SRSC).

Ayenia microphylla A. Gray, Dense ayenia, uncommon to occasional subshrub, DSC, DAR, DCA, 1800–4800 ft; *JF 1124, 1957, 2038, 2172, BGH 632, AMP & SAP 5307, BHW 20620* (SRSC); *DSC & HBC 30627, BHW 10791* (TEX-LL).

§ *Ayenia pilosa* Cristóbal, Hairy or dwarf ayenia, subshrub, 3000 ft; *BHW & LCH s.n.* (BGWMA); *BHW & LCH BG-139* (SRSC).

Tamaricaceae

!!§ *Tamarix aphylla* (L.) H. Karst., Athel tamarisk, saltcedar, locally occasional tree, DSC, RIO, 1800–1900 ft; *BHW 13052* (BIBE); *AMP 3349, BHW 13052* (SRSC); *AMP 3349* (TEX-LL). These large trees were historically planted around developed areas; those in the RGV area are being targeted and removed by NPS exotic plant eradication teams, as are the *Tamarix chinensis*, but they are firmly established in upstream areas and so will likely continue to reestablish along the river corridor into the future.

!! *Tamarix chinensis* Lour., Five-stamen tamarisk, saltcedar, locally abundant tree, DCA, RIO, 1800–ca. 4000 ft; *JF 1346, 2233, 2253, MT 179* (SRSC).

Ulmaceae

Celtis pallida Torr., Spiny hackberry, common shrub or tree, DAR, DCA, RIO, 1800–2800 ft; *CMR 5078* (BGWMA); *JF 2112, TR 80, MT 204 BHW 14048* (SRSC).

§Δ *Celtis reticulata* Torr., Netleaf hackberry, palo blanco, tree. Listed by Amos and Giles (1992) as occurring in Brushy Canyon. Known from BBNP and commonly through the rest of Brewster County.

Urticaceae

+o *Parietaria pensylvanica* Muhl. ex Willd., Pennsylvania pellitory, rare annual herb, DSC, DCA, 3150–3560 ft; *JF 538, 1701* (SRSC).

Verbenaceae

o *Aloysia gratissima* (Gillies & Hook.) Tronc., Beebrush, whitebrush, occasional shrub, DSC, DAR, DCA, 1880–3480 ft; *JF 671, 1362, TR 102* (SRSC).

+o *Aloysia wrightii* A. Heller ex Abrams, Wright beebrush, oreganillo, uncommon shrub, DSC, DCA, SYG/CHP, 3560–5080 ft; *JF 476, 746* (SRSC).

Bouchea spathulata Torr., Spoonleaf, occasional shrub, DSC, DAR, DCA, SYG, 1800–5000 ft; *BA2, DG, TE, & B 4927* (BIBE); *PVW s.n.* (KANU); *BA2 4927, SJ & GJ 6503* (SAT); *JF 170, 857, 1511, MT 1* (SRSC); *BHW 10749, 10766* (TEX-LL).

§ *Glandularia bipinnatifida* (Nutt.) Nutt. var. *ciliata* (Benth.) B.L. Turner [*Glandularia bipinnatifida* (Nutt.) Nutt.], Dakota mock vervain, uncommon perennial herb, DSC, DAR, RIO, 1800–3520 ft; *OES 1492* (BIBE); *HTF 1226, GLW 4466* (SRSC). The varietal status is based on recent chromosome work on this genus (Turner and Powell 2005).

Glandularia quadrangulata (A. Heller) Umber [*Glandularia verecunda* Umber], Beaked verbena, uncommon annual herb, DSC, DCA, RIO, 1800–3300 ft; *CMR 5140* (BGWMA); *JF 618* (BIBE); *CMR 16409* (SAT); *JF 618, HTF 1224* (SRSC); *BHW & RRI 21430* (TEX-LL). The individuals found in BBNP may be more appropriately placed under *Glandularia verecunda* based on different seed structure, with *Glandularia quadrangulata* being a more northerly distributed taxon (Powell in prep., Henrickson 2003).

§ *Glandularia wrightii* (A. Gray) Umber, Wright verbena, pinky, perennial herb; *CMR 16408* (SAT).

Lantana achyranthifolia Desf., Brushland shrubverbena, desert lantana, uncommon to occasional shrub, DSC, DAR, DCA, 1800–2780 ft; *TR 103* (BGWMA); *BA2 4636, 4936* (SAT); *JF 163, 947, 1364, TR 103* (SRSC); *BHW 831a* (TEX-LL).

Lippia graveolens Kunth, Mexican oregano, scented lippia, uncommon shrub, DSC, DAR, DCA, 1800–2350 ft; *DG & TE 4613, EGM 148, BHW 13065* (BIBE); *DG 4613* (SAT); *JF 1080, 1341, 1691, 2032, 2142, AMP s.n., 5306, 5823, BHW 13065, 21202* (SRSC); *BHW 831* (TEX-LL).

Phyla nodiflora (L.) Greene, Turkey tangle frogfruit, "frequent" perennial herb, RIO, DCA, 1800–2300 ft; *AL 321, BHW 833* (BIBE); *JF 2243, OCW 510, BHW 20435* (SRSC).

§ *Tetraclea coulteri* A. Gray, Coulter wrinklefruit, stinkweed, "infrequent" perennial herb, 2250 ft; *BRM 3209, CMR 5073* (BGWMA); *BA2 5717* (SAT); *BHW & LCH BG-184* (SRSC).

Verbena neomexicana (A. Gray) Small, Hillside vervain, New Mexico verbena, occasional to "abundant" perennial herb, RIO, DCA, 1800–? ft; *BRM 3047, CMR 11635* (BGWMA); *JF 2265* (SRSC).

Violaceae

Hybanthus verticillatus (Ortega) Baill., Babyslippers, uncommon to rare perennial herb, DSC, SYG, 3000–4900 ft; *JF 220, 1322, 2170, BHW 10895* (SRSC).

Viscaceae

Phoradendron hawksworthii (Wiens) Wiens , Hawksworth mistletoe, rare subshrub, DSC/SYG, 4160 ft; *JF 1896* (SRSC).

Phoradendron tomentosum (DC.) Engelm. ex A. Gray, Christmas mistletoe, uncommon subshrub, DSC, DCA, 2780 ft; *CMR 5097* (BGWMA); *JF 182* (SRSC); *AMP & SAP 4301* (SRSC & TEX-LL).

Phoradendron villosum Nutt., Oak or Cory mistletoe, uncommon subshrub, SYG/CHP, 2300–5000 ft; *PVW s.n.* (KANU); *JF 769, 1209, BHW 10845, 10846, OCW 505, BHW & LCH BG-145* (SRSC).

Vitaceae

+ *Cissus incisa* (Nutt. ex Torr. & A. Gray) Des Moul., Sorrelvine, ivy treebine, rare perennial woody vine, DSC, DAR, 2050–3740 ft; *JF 232, 1682* (SRSC).

§ *Vitis arizonica* Engelm., Canyon grape, "abundant" perennial woody vine, RIO, 1800 ft; *EGM 156, BHW 13038* (BIBE); *BHW 13038, GLW 4489* (SRSC).

Zygophyllaceae

Guaiacum angustifolium Engelm., Guayacan, Texas lignum-vitae, common shrub, DSC, DAR, DCA, RIO, 1800–3280 ft; *CMR 5033* (BGWMA); *JF 224, 690, 2111, TR 96, BHW 18413* (SRSC).

§ *Kallstroemia grandiflora* Torr. ex A. Gray, Arizona poppy, "infrequent" annual herb, DSC, DCA, 1800–2320 ft; *BLT & MT2 97-336, BHW & MCJ 16867* (SRSC); *EGM 53, BLT & MT2 97-336* (TEX-LL)

o *Kallstroemia hirsutissima* Vail, Hairy caltrop, uncommon annual herb, DSC, 1900–3000 ft; *JF 199, 219, BHW 13066* (SRSC).

§ *Kallstroemia parviflora* Norton, Warty caltrop, annual herb; *BHW & LCH BG-197* (SRSC).

Larrea tridentata (Sessé & Moc. ex DC.) Coville, Creosote, gobernadora, abundant shrub, DSC, DAR, 1800–3560 ft; *ACK 829* (BIBE); *JJ 40, JT 30* (SAT); *JF 606* (SRSC); *DS 1091* (TEX-LL).

! *Tribulus terrestris* L., Goathead, puncturevine, "infrequent to frequent" annual herb, RIO, 1800 ft; *BA2, DG, TE, & PC 4607, EGM 157* (BIBE); *BA2 4607* (SAT); *JF 2227, BHW 23036, BHW & MCJ 16850* (SRSC).

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DISTRIBUTION AND TAXONOMY OF *SYMPHYOTRICHUM SERICEUM* AND *S. PRATENSE* (ASTERACEAE: ASTEREAE)

Ronald L. Jones
Dept. of Biological Sciences
521 Lancaster Avenue
Eastern Kentucky University
Richmond, Kentucky 40475, U.S.A.

C. Theo Witsell
Arkansas Natural Heritage Commission
1500 Tower Building
323 Center Street
Little Rock, Arkansas 72201, U.S.A.

Guy L. Nesom
2925 Hartwood Drive
Fort Worth, Texas 76109, U.S.A
guynesom@sbcglobal.net; http://guynesom.com.

ABSTRACT

Symphyotrichum sericeum and *S. pratense* are distinct, non-intergrading species primarily of the central U.S.A., sympatric only in Texas. The densest distribution of *S. sericeum* is in north-central states, with disjunct populations and population systems extending southward to Arkansas, Oklahoma, and Texas. The densest distribution of *S. pratense* is in Texas, southern Arkansas, and Louisiana, with disjuncts extending to Alabama, Florida, Georgia, Kentucky, Mississippi, Tennessee, and Virginia, with an historical record from North Carolina. Specimens from these disjunct sites in the southeastern U.S., some of which are still being listed as *S. sericeum* on state checklists and rare species reports, are here treated as *S. pratense*. *Symphyotrichum sericeum* consists largely of diploid populations, while both tetraploid and diploid populations occur in *S. pratense*. County-level distributions of both species are mapped. *Symphyotrichum sericeum* is state-listed in 4 states and *S. pratense* in 7 states.

RESUMEN

Symphyotrichum sericeum y *S. pratense* son especies distintas, que no se intergradan, primariamente del centro de U.S.A., simpátricas sólo en Texas. La distribución más densa de *S. sericeum* está en los estados del centro-norte, con poblaciones disyuntas y sistemas de poblaciones que se extienden hacia el sur hasta Arkansas, Oklahoma, y Texas. La distribución más densa de *S. pratense* está en Texas, sur de Arkansas, y Louisiana, con disyunciones que se extienden hasta Alabama, Florida, Georgia, Kentucky, Mississippi, Tennessee, y Virginia, con una cita histórica de North Carolina. Especimenes de estas disyunciones en el sudeste de U.S., algunos de los cuales aún se listan como *S. sericeum* en listados estatales y citas de especies raras, se tratan aquí como *S. pratense*. *Symphyotrichum sericeum* consiste mayormente en poblaciones diploides, mientras que en *S. pratense* se encuentran tanto poblaciones tetraploides y diploides. Se aportan mapas de distribución a nivel de condado de ambas especies. *Symphyotrichum sericeum* está en las listas estatales de cuatro estados y *S. pratense* en 7.

Symphyotrichum sericeum (Vent.) Nesom and *S. pratense* (Raf.) Nesom are two closely related taxa of central and eastern United States. In most treatments they have been maintained as distinct species (e.g., Correll & Johnston 1970, Cronquist 1980, Jones 1990, Nesom 1994, Brouillet et al. 2006). When the taxa are considered to be conspecific (see Wunderlin & Hansen 2004), *S. pratense* is treated as *S. sericeum* var. *microphyllum* (DC.) Wunderlin & B.F. Hansen. *Symphyotrichum pratense* was known for many years as *Aster phyllolepis* Torr. & A. Gray. *Symphyotrichum sericeum* is generally distributed in the central states, from Texas to North Dakota and southern Canada, to western Michigan. *Symphyotrichum pratense* is largely concentrated in eastern Texas and western Louisiana. Populations of plants in this complex that are disjunct further eastward—to Florida, Virginia, and Kentucky—are somewhat intermediate in phyllary morphology and have been variously treated as *S. sericeum*, *S. pratense*, or *S. sericeum* var *microphyllus*, and a number of states treat these often widely scattered populations as state-rarities. Chromosome counts also need clarification, as both ploidy levels ($2n = 10$ and $2n = 20$) have been published for both taxa (Brouillet et al. 2006). The objective of this paper is to update available information on this complex, clarify geographical distributions, point out distinguishing features, identify typical habitats and associates, review available chromosome information, and summarize the state-rarity status of the taxa.

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The present study provides a detailed view of the geographic distribution of *Symphyotrichum sericeum* and *S. pratense*, based primarily on a study of herbarium specimens from BRIT-SMU, EKY, GA, LSU, MO, NCU, NLU, TENN, TEX-LL, UNC, VDB, and VPI. Maps are augmented by records from various published sources. The available literature on habitats, associates, and chromosome numbers was also reviewed. A new chromosome report from a Kentucky population is based on mitotic counts from root tip squashes from germinating achenes. The key is based on a detailed examination of morphological characteristics of herbarium specimens from across the ranges of the two taxa.

SYMPHYOTRICHUM SERICEUM

Distribution and Habitat.—The primary distribution of *Symphyotrichum sericeum* is from Arkansas and Oklahoma to southern Canada to western Michigan and Indiana, with disjunct populations in central Texas (Fig. 1). Over the larger part of its range, *S. sericeum* occurs in a variety of habitats, e.g., dunes, sandy woods, glades, sandstone glades, over granite outcrop—but typically associated with seasonally dry, open to semi-open habitat. *Symphyotrichum sericeum* in Texas mostly occurs on the Edwards Plateau, where it grows on limestone hills, commonly on open, rocky slopes and roadbanks. An early collection supposedly made far to the east (**Harris Co.:** *Lindheimer 78*, BRIT) is similar in every respect to Edwards Plateau plants and may be mislabeled. Swink and Wilhelm (1994) list a number of associates of this species in Illinois, including *Amorpha canescens*, *Schizachyrium scoparium*, and *Bouteloua curtipendula* in dry hill prairies, and *Anemone cylindrica*, *Liatris aspera*, *Liatris cylindracea*, and *Spiranthes cernua* in sand barrens sites near Lake Michigan. In Wisconsin it occurs at dry prairie sites on hillsides, outcrops, and bluffs, sometimes under oaks, jack pine, or red cedar, but usually in the open in habitats dominated by *Schizachyrium scoparium*, with *Asclepias viridiflora*, *Dalea purpurea*, and *Brickellia eupatorioides* (Cochrane & Iltis 2000). In Manitoba the species occurs in remnant tall-grass prairie sites and in openings in *Quercus macrocarpa*/*Populus tremuloides* woodlands (Foster & Hamel 2006).

The species is primarily associated with the Central Lowlands Physiographic Province in the U.S., but it also occurs in the Ozark Plateau Province of Arkansas and Missouri. A recent collection of *Symphyotrichum sericeum* from open shale barrens on a southwest-facing slope in central Arkansas, is apparently the first record from the Ouachita Mountains Province. This site is disjunct from the nearest populations about 155 km to the northeast on the Ozark Plateau. Voucher: **Garland Co.:** Ouachita Mountains, Ouachita National Forest, steep S-facing shale barrens (Mazarn Formation) on upper slope, east of and above Walnut Creek near point at which it flows into Lake Ouachita, Crystal Springs 7.5' quadrangle, steep glades, elev. 750 ft, hundreds of plants in high quality shale barrens, 29 Sep 2006, *Witsell 06-471* (ANHC,BRIT, UARK). A second population was subsequently found in similar habitat 1.9 km northwest of the above site.

Chromosome Numbers.—There are about a dozen published diploid counts for *Symphyotrichum sericeum*, these mostly from the northern portions of its range (Jones 1980; Semple & Brouillet 1980; Semple & Chmielewski 1987; Semple et al. 1989; Semple et al. 2002), with the most southerly count from Izard Co., Arkansas (Sherif et al. 1983). There is apparently only a single report of a tetraploid count (Löve 1982) for *S. sericeum*, this count from Canada; there are also diploid counts from this same vicinity (J. Semple, pers. comm.).

Taxonomy.—Brouillet et al. (2006) treated *Symphyotrichum lucayanum* (Britt.) Nesom as a synonym of *S. sericeum*, but *S. lucayanum* is here considered to be more closely related to *S. concolor* (L.) Nesom, based on their similarities in capitulescence and phyllary morphology and their closer geographical proximity. The latter is widespread in the southeastern U.S.A. *Symphyotrichum lucayanum* was treated by Nesom (1994) as a distinct species, based on its very loosely racemiform capitulescence with interspersed leaves only slightly reduced or not at all from the proximal cauline, different from the more densely congested, bracteate capitulescence of *S. concolor*. Turner (1982) treated the taxon as a synonym of *Aster concolor* L., and the type of *Aster lucayanum* Britt. (*Britton & Millspaugh 2448*, NY!) was annotated by W.T. Gillis in 1974 as *A. concolor*.

State-Rarity.—*Symphyotrichum sericeum* is currently ranked as S2 (Threatened or Rare) in Arkansas, Indiana, Michigan, and North Dakota (NatureServe 2008). It is listed as Nationally Threatened in Canada

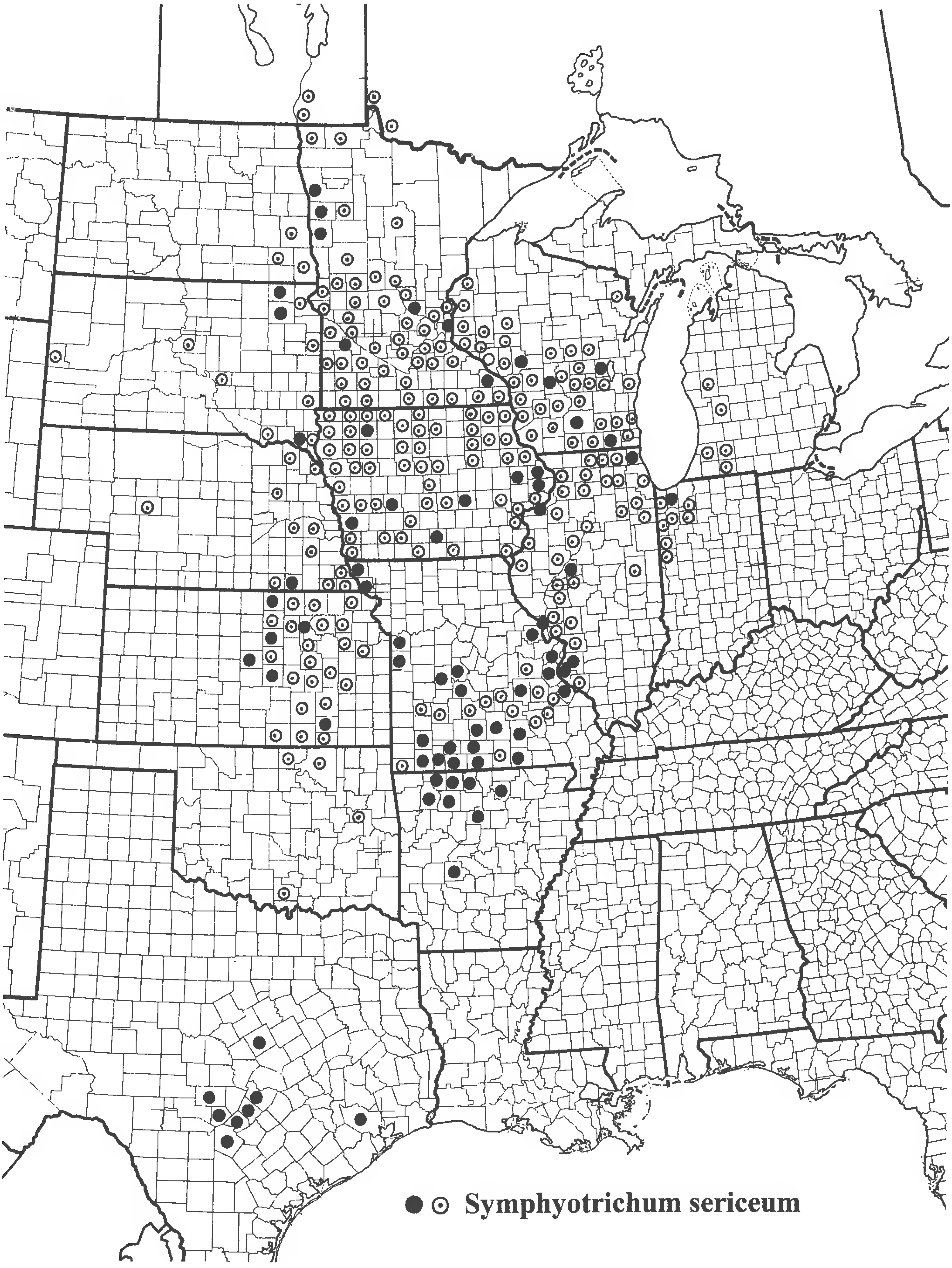

FIG. 1. Distribution of *Symphyotrichum sericeum*. Solid circles are from vouchered observations; dotted circles are from literature records.

(Foster & Hamel 2006). We could find no substantiation of the occurrence of *S. sericeum* in Georgia, Ohio, or Tennessee, where indicated to occur by Brouillet et al. (2006) and NatureServe (2008).

SYMPHYOTRICHUM PRATENSE

Distribution and Habitat.—The densest distribution of *Symphyotrichum pratense* is in Texas, Louisiana, and southern Arkansas—scattered, disjunct clusters of populations occur eastward over a wide geographic range and in a variety of physiographic provinces (Fig. 2). *Symphyotrichum pratense* in Texas characteristically occurs in sandy soil (sand, sandy loam, sandy clay, silty clay, silty clay-loam), being largely restricted to the following natural regions: Piney Woods, Oak Woods and Prairie, Gulf Coast Prairie and Marshes, and Blackland Prairie. Within these regions, it is less frequent in blackland prairie: e.g., **Texas. Dallas Co.:** *Lundell 12032* (LL, SMU). Shinners (1950), who recognized the legitimacy of the Rafinesque name ahead of the Torrey & Gray name, described this species as "a frequent and showy plant of open oak woods and transition-belt prairies thoughout east Texas ..." In Texas, *S. pratense* also occurs in longleaf and loblolly pine areas and in coastal prairie grassland, and it has been collected from fields, roadsides, clearings, and fencerows.

In Louisiana the plants occur in pine flatwood sites, blackland prairie, chalk hills, and calcareous clays, as well as along dry roadsides. A blackland prairie locality for *Symphyotrichum pratense* is on the "Kieffer Prairie:" **Winn Par.:** *Brown 8220* (SMU) and five other collections from the same locality (LSU Herbarium Online Database 2008). At the Kieffer Prairie *S. pratense* grows with associates such as *Schizachyrium scoparium, Andropogon gerardii, Sorghastrum nutans, Echinacea pallida, Oligoneuron rigidum,* and *Vernonia missurica* (USDA Forest Service 2008).

In the Gulf Coastal Plain of Arkansas, typical habitat for *Symphyotrichum pratense* is open saline barrens—treeless openings in *Pinus taeda/Quercus similis* flatwoods with clay soils containing high levels of sodium and/or magnesium. Eric Sundell, who first discovered the species in Arkansas at the Warren Prairie (Sundell 1983), noted that the plants occurred with prickly pear and dwarf palmetto and that a number of other rare species were associated with these sites, including *Geocarpon minimum* and *Schoenolirion wrightii*. The USDA Plants website (USDA, NRCS 2008) lists Izard and Newton counties in Arkansas for *S. pratense*, but these records from northern Arkansas are based on collections of *S. sericeum*.

Eastward (to Alabama, Florida, Georgia, Kentucky, Mississippi, Tennessee, and Virginia), *Symphyotrichum pratense* occurs mostly in calcareous habitats, e.g., chalk barrens, cedar glades, and limestone outcrops. Kral (1981) reported on the species at Coastal Plain sites in Alabama (Sumter Co.) and Florida (Gadsden Co.) and noted that the plants in Alabama were found in blackland prairie patches and that those in Florida were found at rocky calcareous outcrops in association with *Schoenus nigricans*, a plant more normally found near the coast. The species subsequently was discovered in Decatur Co., Georgia, just across the state line from Gadsden Co., in calcareous glades on a bluff: **Decatur Co.:** *Godfrey & Gholson 80099* (GA). In Mississippi the species occurs in association with calcareous chalky outcrops (L. McCook, pers. comm.). The central Alabama and Mississippi populations are located in the Black Belt prairie lands (see Barone 2005). The most northerly populations in Alabama occur in limestone prairie barrens within the Highland Rim province, along with many other rare species, including *Dalea gattingeri, Leavenworthia alabamica, Cypripedium candidum, Eriogonum longifolium* var. *harperi, Schoenolirion croceum,* and *Spiranthes magnicamporum* (Webb et al. 1997).

At its most northerly range limits in Kentucky, *Symphyotrichum pratense* is found in glades or barrens habitats of the Interior Low Plateaus (chiefly Highland Rim sites) with *Juniperus virginiana* and *Quercus marilandica* as the woody dominants and with *Andropogon gerardii, Schizachyrium scoparium, Sorghastrum nutans, Sporobolus compositus,* and *S. vaginiflorus* as the conspicuous grasses. These habitats often contain a variety of other rare or infrequent plants, such as *Cypripedium candidum, Echinacea pallida, Liatris aspera, Liatris cylindracea, Lithospermum canescens, Silphium pinnatifidum, Dalea candida, Dalea purpurea,* and *Physostegia virginiana* (Cranfill 1991; Kentucky State Nature Preserves Commission 2008). The barrens sites in Tennessee (Highland Rim and Appalachian Plateau sites) and in southwestern Virginia (Valley and Ridge)

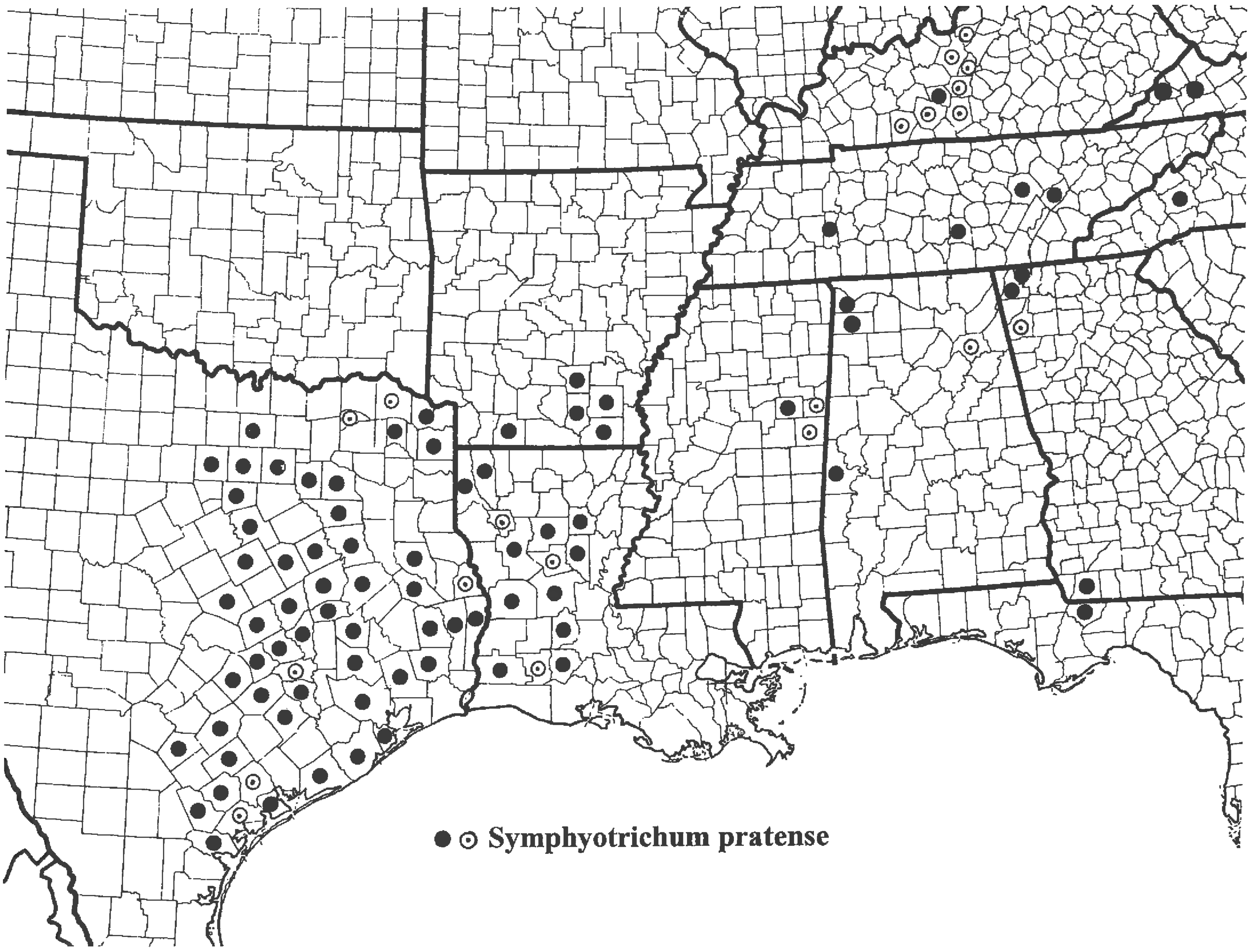

Fig. 2. Distribution of *Symphyotrichum pratense*. Solid circles are from vouchered observations; dotted circles are from literature records.

are very similar to the Kentucky sites and also contain a number of very rare species (DeSelm 1990; Ludwig 1999; Tennessee Natural Heritage Program 2008). In northern Georgia the plants occur at both Appalachian Plateau and at Valley and Ridge sites (T. Patrick, pers. comm.). In the Coosa river watershed of Georgia, *S. pratense* occurs in limestone glades; other species associated with this habitat include *Asclepias hirtella*, *Baptisia australis*, *Buchnera americana*, *Dalea gattingeri*, *Echinacea pallida*, *Hypericum dolabriforme*, *Hypericum sphaerocarpum*, *Liatris squarrosa*, and *Spiranthes magnicamporum* (Georgia Department of Natural Resources 2007).

Recent investigations of dolomite and limestone barrens in southwestern Virginia have discovered several populations of *Symphyotrichum pratense* -- initially reported by Ludwig (1999), subsequently treated by Brouillet et al. (2006), Weakley (2007), and Virginia Botanical Associates (2008). We have studied the following vouchers: **Russell Co.:** 1 km E of Carterton, one-acre barren at top of SW-facing slope on W end of a short ridge, dense grass cover with dolomitic limestone cobbles, 20 May 1996 [not yet in flower], *Wieboldt 9415* (VPI); river knob 1 km E of Carterton, top of SW-facing hardwood slope, substrate cobbly with dolomitic (?) limestone, 2100 ft, dominant species with *Liatris aspera* and *Andropogon gerardii*, scattered over most of one-acre barren, 17 Sep 1996, *Wieboldt 9605* (VDB, VPI); E side of Mill Creek where it cuts through ridge between Clinch River and Reeds Valley, ca. 1.9 km N of Jessees Mill, SW-facing limestone hillside in open grassland dominated by *Schizachyrium scoparium*, 2040 ft, ca. 20 plants, 11 Sep 1996, *Ludwig 3082* (VPI). **Wise Co.:** *Fleming 14122* (GMUF). Ludwig (1999) noted that this species has been found at six Russell County sites.

Chromosome Numbers.—The first report of the tetraploid level of 2*n*=20 for *Symphyotrichum pratense* was from Gonzales Co., Texas, by Semple and Brouillet (1980), who noted that a diploid count had been made earlier for the species, but that report was unvouchered and part of a 1945 embryological study by German anatomists. Semple and Chmielewski (1987) published diploid counts for plants from Grimes and Walker counties in Texas and a tetraploid count for plants in Milam Co., Texas. Two years later Semple et. al. (1989), reported a diploid count of 2*n*=10 for plants from Gadsden Co., Florida. In addition, we report a previously unpublished 2*n*=20 count for *S. pratense*: **Kentucky. Hardin Co.:** cedar glade off KY 2762, 6 Nov 1987, *R.L. Jones 5457* (EKY).

Taxonomy.—In the main part of the range of *Symphyotrichum pratense*, the plants typically have phyllary surfaces mostly glabrous and strongly contrasting with the spreading-ciliate margins. Phyllaries of the Virginia plants are unusual, having densely sericeous surfaces, with or without strongly ciliate margins, but resemble typical *S. pratense* of Texas and Louisiana in the proximal indurate portion of the phyllary being relatively short, the distal leafy portion being relatively broad and long, and the overall phyllary length about 1.5 cm. Their geographic position also obviously suggests that they are part of *S. pratense*. Some plants from Tennessee are similar in their phyllary features (e.g., **Roane Co.:** *Morton 1307*, SMU).

The description of *Aster montanus* Nutt. seems to refer to *Symphyotrichum pratense*; Nuttall noted that it was "nearly allied to the preceding [*Aster sericeus*], but distinct." Torrey and Gray (in Fl. N. Amer.) treated it as *A. sericeus* var. β. They also noted that the species was known from "Tennessee and North Carolina near the mountains." On Nuttall's 1816 trip, he crossed from Tennessee to Asheville, N.C., and went on to Rutherfordton and Morganton (Graustein 1967). Gray (in Synop. Fl. N. Amer.) formalized the name at varietal rank, as *Aster sericeus* var. *montanus* (Nutt.) Gray, noting that the involucre is "sometimes glabrate and villose-ciliate; approaching the next species [*A. phyllolepis*]." An image of the holotype of *A. montanus* was obtained from PH, and an examination indicates that the involucral widths are about 2 cm wide, much larger than typical *S. sericeum*, and we therefore place this name in the synonomy of *S. pratense*.

Today neither *S. sericeum* nor *S. pratense* is known to occur in North Carolina. Gray (in Fl. N. Amer.) listed North Carolina as included in the range of *A. sericeus* var. β, and later (in Synop. Fl. N. Amer.), he specified Buncombe County as the site of the collection. The specimen upon which Gray apparently based his comment was located at NY, and an image was obtained. The sheet bears three plants from two different areas—two are from Minnesota and identified as *Aster sericeus*, while the other was collected from "Buncombe, North Carolina, *Gibbes*" and identified as "*A. sericeus* β. (*montanus* Nutt.)." This latter specimen exhibits the large heads of *S. pratense*, and is here assigned to that taxon; it represents the only known record of the species from North Carolina. *S. pratense* has not been subsequently rediscovered in the state and can be assumed to be extirpated there.

Aster montanus Nutt., Gen. N. Amer. Pl. 2:156. 1818 (non *A. montanus* All. 1785). *Aster sericeus* var. *montanus* (Nutt.) A. Gray, Synopt. Fl. N. Amer. 1, part 2:179. 1884. *Lasallea nuttallii* Greene [nom. nov.], Leafl. Bot. Observ. Crit. 1:5. 1903. USA. Tennessee. No other collection data, [*T. Nuttall s.n.*, September to early October 1816, fide Graustein 1967], annotated in Nuttall's handwriting as "*Aster montanus*" (HOLOTYPE: PH, digital image!). Nuttall's protologue: "HAB. On the mountains of Tennessee and North Carolina, rare. (Near Asheville and Morganton)."

When these disjunct populations of *Symphyotrichum pratense* were first discovered in eastern U.S., especially at the more northerly sites in Alabama, Tennessee, and Kentucky, they were often identified as *S. sericeum*. They are still listed as such in several state natural heritage databases. We now confirm all examined specimens from Alabama, Florida, Georgia, Kentucky, Mississippi, North Carolina, Tennessee, and Virginia as *S. pratense*.

State-Rarity.—*Symphyotrichum pratense* is generally rare outside its main range in Texas and Louisiana — it is currently considered Threatened (S2) in Arkansas, Special Concern (S3) in Kentucky, and S1 (critically imperiled) in Alabama, Georgia, Mississippi, Tennessee, and Virginia (NatureServe 2008). Although there is only one known county of occurrence in Florida (the only state where it still is treated as a variety of *S. sericeum*, *S. pratense* is currently not listed among that state's rare species (Florida Natural Areas Inventory 2008).

Morphological Criteria for Distinguishing the Taxa.—Our examination of specimens from throughout much of the ranges of the two taxa indicates that they can be reliably distinguished as follows:

1. Phyllaries densely sericeous, vestiture of margins similar to surfaces, not spreading ciliate; terminal, green, pubescent portion of largest phyllaries 1/4–1/3(–1/2) the total phyllary length, usually distinctly shorter than the proximal, indurate and glabrate portion; middle phyllaries mostly ≤ 7 mm long and ≤ 2 mm wide, averaging 6(–8) mm long and 2(–3) mm wide; involucral height mostly < 10 mm (7–11 mm) high ____ **Symphyotrichum sericeum**
1. Phyllaries with abaxial faces usually glabrous to glabrate, less commonly sparsely strigose sericeous (rarely densely sericeous), margins ciliate with thick-based, spreading hairs 0.5–1.0 mm long, much longer than those on the surfaces; terminal, green, pubescent portion of largest phyllaries 2/3–3/4 the total phyllary length, longer than the proximal, indurate and glabrate portion; middle phyllaries mostly ≥ 8 mm long and ≥ 2.5 mm wide, averaging 9(–14) mm long, and 3(–5) mm wide; involucral height mostly ≥ 10 mm (8–15 mm) high ____ **Symphyotrichum pratense**

CONCLUSION

Symphyotrichum pratense and *S. sericeum* are distinct species of central and eastern U.S. They are largely allopatric in distribution, and occur sympatrically only in Texas, where *S. pratense* is common and *S. sericeum* rare. *Symphyotrichum pratense* is associated with a range of physiographic provinces—it is chiefly Coastal Plain in distribution, but its range extends to the Interior Low Plateaus, the Appalachian Plateau, and the Valley and Ridge. There is an historical record from the Blue Ridge of North Carolina. *Symphyotrichum sericeum* is largely associated with the Central Lowlands Province and the Ozark Plateau, and only sporadically into adjacent provinces to the south, north, and west. Disjunct populations and population systems are a prominent feature of the biology of both taxa. There is some intermediacy in phyllary pubescence in the easternmost disjunct populations, but these features could be interpreted as resulting from local genetic drift in populations far removed from the main range of the species, and there is no evidence of any significant gene interchange between the taxa. The available evidence indicates that *S. sericeum* consists of diploid populations (with the exception of one anomalous report) and that *S. pratense* contains populations at both ploidy levels. *Symphyotrichum sericeum* is generally common throughout much of its range, considered rare only in the states at the eastern and southern periphery of its range (Michigan, Indiana, and Arkansas), and is Nationally Threatened in Canada. Outside of Texas and Louisiana, *S. pratense* is a rare plant and is considered critically imperiled in several states (Alabama, Georgia, Mississippi, Tennessee, and Virginia). The identity of these disjunct eastern populations has been the source of some confusion in the past — they have been variously treated by the different states as *S. pratense* or *S. sericeum*, and this latter name continues to be used by some eastern states for their rare species lists. Our study concludes that all specimens examined from populations in Alabama, Florida, Georgia, Kentucky, Mississippi, North Carolina, Tennessee, and Virginia, are *S. pratense*.

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BOOK NOTICE

Rachel Wilson (ed.). 2007. **Sweeteners Handbook, Third Edition.** (ISBN 978-1-905224-42-5, hbk.). Blackwell Publishing Professional, 2121 State Avenue, Ames, Iowa 50014-8300, U.S.A. (**Orders:** www.blackwellfood.com, 1-800-862-6657, 1-515-292-3348 fax). $169.99, 304 pp., b/w figures and tables, 6" × 9".

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RANUNCULUS FICARIA (RANUNCULACEAE), NATURALIZED IN TEXAS

Guy L. Nesom

2925 Hartwood Drive
Fort Worth, Texas 76109, U.S.A.
guynesom@sbcglobal.net

ABSTRACT

Ranunculus ficaria is naturalized along a creek in Tarrant Co, Texas. The plants produce axillary bulbils and infertile achenes and perhaps are best identified as subsp. *bulbifera*, although other morphological features do not closely accord with previous descriptions of that subspecies.

KEY WORDS: *Ranunculus ficaria*, naturalized, Texas

RESUMEN

Ranunculus ficaria está naturalizado a lo largo de un arroyo en Tarrant Co, Texas. Las plantas producen bulbillos axilares y aquenios infertiles y quizás estén mejor identificados como subsp. *bulbifera*, aunque otras características morfológicas no estén muy de acuerdo con las descripciones previas de esa subespecie.

A population of *Ranunculus ficaria* L. (lesser celandine, fig buttercup) was discovered in flower immediately adjacent to Overton Creek in Fort Worth's Overton Park, near the center of the city. The creek at this point runs through a broad but relatively steep-sided ravine and is about three miles above confluence with the Trinity River. Tributaries of Overton Creek pass through several miles of urban neighborhood upstream from this area. The creek commonly rises beyond its banks in heavy rain.

Thirty discrete plants, clearly naturalized, grow in an area of about 30 square feet—the largest produced at least 20 flowers. A second population of five scattered plants occurs on the stream terrace about 300 yards downstream.

Voucher Specimen: **TEXAS. Tarrant Co.:** Fort Worth, Overton Park between the TCU campus and Hulen Street, Overton Creek parallel to Shady Creek Drive, immediately adjacent to the creek on the wet, sandy terrace, first seen in flower 2 Mar, collected 8 Mar 2008, axillary bulbils abundantly in production by 2 Apr, *Nesom FW08-1* (BRIT, MO, NCSC, NCU, TEX).

The Overton Creek plants arise from tuber-producing fibrous roots and produce dark green, glabrous, ovate and deeply cordate but otherwise entire (to faintly crenate) basal leaves and solitary, yellow flowers on erect to ascending leafless peduncles. The habitat is typical for the species—where naturalized elsewhere in North America, the plants occur on shaded stream banks, floodplains, low woods, and moist disturbed areas. "Flowering usually occurs from late winter through mid-spring (March through May), depending on conditions. Afterwards, the above-ground portions die back" (Swearingen 2005). *Ranunculus ficaria* is a beautiful horticultural species, and many photos are available on the internet.

Sell (1994) distinguished five subspecies based primarily on leaf and flower size, achene fertility, and whether or not axillary bulbils are produced after flowering. Among the five subspecies, only subsp. *bulbifera* (Marsden-Jones) Lawalree (as "subsp. *bulbilifer* Lambinon") and subsp. *ficariiformis* (F.W. Schultz) Rouy & Fouc. were described by Sell as producing bulbils, and of these two, only subsp. *bulbifera has infertile, glabrous achenes*. The Overton Creek plants produce axillary bulbils and infertile achenes and probably are best identified as subsp. *bulbifera*, but otherwise they are not a clear morphological match for any of the subspecific taxa in Sell's key. The leaves are numerous and densely crowded at the base on short stems. Most leaves are ca. 6–7 cm long and 5–5.5 cm wide, ranging smaller to 3 × 3 cm, on petioles 8–10 cm long. The flowers are ca. 2.5–4 cm in diameter with 7–9 petals 15–19 mm long, 6–8 mm wide. Pollen (2 plants) is ca 70% viable, as judged by uniform size and full-staining in lactophenol-cotton blue; the remaining 30%

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of the grains are non-staining and distinctly smaller (and highly variable in size). All achenes apparently are glabrous and infertile. Axillary bulbils were not present at the time of collection (8 March) but were in abundant production by 2 April—they are whitish, conic-cylindric to short-cylindric, and essentially without surface features. Superficially, at least, the axillary bulbils are very similar to the root tubers. Many stems and leaves had at least begun to wither by 5 May, with the axillary bulbils loosened and easily detached.

Confidence in identification of infraspecific taxa is further tempered by Whittemore's observations (1997): "The species is extremely variable (especially in leaf size and stem posture), and many attempts have been made to divide it into varieties or subspecies (see Sell 1994). The different forms, however, intergrade extensively and the varieties are often impossible to distinguish." Sell himself noted (p. 47) that "a large proportion of herbarium specimens cannot be determined with certainty" and relied on field experience in the British Isles and on published literature to summarize distributions of the infraspecific taxa.

Sell (1994) noted that "all the subspecies can spread by tubers ('Clones of all the subspecies can be produced by division of the root tubers.'), two spread by axillary bulbils, and all except subsp. [*bulbifera*] can spread by seed." Both the tubers and bulbils are easily carried downstream during flood events (Bargeron et al. 2003). Bulbils are produced near the end of flowering or in fruit maturation, and Sell noted that the five taxa can be recognized "if cultivated, or if examined at intervals through their flowering and fruiting periods." Detailed observations of this nature, however, apparently have not been recorded in North America—Magee and Ahles (1999) and Rhoads and Block (2007) unequivocally specify that the plants produce bulbils, but other U.S.A. floras note that bulbils are produced "sometimes" or "often." Only Magee and Ahles have identified the plants to infraspecific rank (as subsp. *bulbifera*).

Ranunculus ficaria is native to Europe, northern Africa, and western Asia. In North America it is naturalized in Oregon, Washington, and British Columbia and from Missouri, Tennessee, and Virginia northward to Ontario, Quebec, and Newfoundland (PLANTS Database 2008). The Texas plants are the southernmost known for the species as naturalized in the U.S.A. It is reported to be invasive in Connecticut, Delaware, Maryland, New Jersey, Oregon, Pennsylvania, Virginia, Wisconsin, West Virginia, and the District of Columbia (Plant Conservation Alliance 2007).

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PASPALUM VAGINATUM (POACEAE), A NEW THREAT TO WETLAND DIVERSITY IN SOUTHERN CALIFORNIA

Richard E. Riefner, Jr.
Research Associate
Rancho Santa Ana Botanic Garden
1500 North College Avenue
Claremont, California 91711-3157, U.S.A.
rriefner@earthlink.net

J. Travis Columbus
Research Scientist
Rancho Santa Ana Botanic Garden
1500 North College Avenue
Claremont, California 91711-3157, U.S.A.
j.travis.columbus@cgu.edu

ABSTRACT

Paspalum vaginatum, a warm-season perennial grass known from tropical and subtropical regions around the world, is reported for the first time for California. We review its distribution, ecology, anthropogenic uses, invasive status, and biological traits promoting its invasive behavior worldwide and in southern California, where it likely arrived as a purposeful human introduction in the 1970s and 1980s. Anthropogenic disturbances, its widespread use in the turf industry, and broad ecological tolerances help to explain its explosive spread and rapid establishment. *Paspalum vaginatum* is now widespread and often highly invasive in estuarine wetlands in southern California. Our preliminary observations, and anecdotal evidence and quantitative data gathered in other countries suggest its impacts to native ecosystems are similar to those of the better-documented nonnative cord grasses (*Spartina* spp.). Accordingly, the long-term consequences of *P. vaginatum* invasions could pose a serious threat to native biodiversity and ecosystem function of estuarine wetlands in southern California. Likely unrecognized in the field for decades, the presence of *P. vaginatum* indicates that focused floristic and taxonomic studies are urgently needed to thoroughly document the nonnative flora of wetland communities throughout urbanized southern California.

KEY WORDS: biodiversity, ecosystem transformers, estuarine wetlands, invasive plants, mudflats, *Paspalum vaginatum*, salt marsh, seashore paspalum, wildland-urban interface

RESUMEN

Paspalum vaginatum, una hierba perenne de clima cálido procedente de las regiones tropicales y subtropicales del mundo, se cita por primera vez en California. Revisamos su distribución, ecología, usos antropogénicos, estatus invasivo y los rasgos biológicos que promueven su comportamiento invasivo en el mundo y en el sur de California, donde probablemente llegó debido a la introducción humana deliberada en las décadas de los 1970 y 1980. Las alteraciones antropogénicas, su uso generalizado en la industria del césped y su amplia tolerancia ecológica permiten explicar su propagación explosiva y su rápido establecimiento. *Paspalum vaginatum* está actualmente ampliamente propagada, y con frecuencia con carácter altamente invasivo, en los humedales de los estuarios del sur de California. Nuestras observaciones preliminares, así como la evidencia anecdótica y los datos cuantitativos acumulados en otros países, indican que su impacto en ecosistemas nativos o autóctonos es similar a aquel de los mejor documentados pastos cordón no nativos (*Spartina* spp.). Por lo tanto, las consecuencias a largo plazo de las invasiones de *P. vaginatum* podrían plantear serias amenazas a la biodiversidad nativa y a las funciones del ecosistema de los humedales de los estuarios del sur de California. La presencia de *P. vaginatum*, probablemente no reconocida en el campo por décadas, indica que urgentemente se necesitan llevar a cabo estudios de floricultura y taxonomía orientados para documentar minuciosamente la flora no nativa de las comunidades de humedales a lo largo de las zonas urbanas del sur de California.

INTRODUCTION

Plant invasions are a major issue for ecosystems around the world (Williamson 1996; Gurevitch & Padilla 2004). The globalization of trade, rapidly expanding urbanization, intensive agriculture and horticultural practices, increasing degradation and fragmentation of natural habitats, biogeographical factors, and climate change are some of the driving forces that increase the movement of species around the world (Mooney & Hobbs 2000; Vila & Pujadas 2001; Myers & Bazely 2003; Pyšek & Richardson 2006). As a result, the flora in many regions of the United States, including California, is now rich in nonnative (alien, exotic) plants (Westbrooks 1998; Bossard & Randall 2007).

Invasive plant species reproduce in very large numbers, are superior competitors, and have the potential to spread across large areas and at considerable distances from parent plants (Richardson et al. 2000). Environmental plant pests (species that affect the loss of native biodiversity) and ecosystem transformers

(species that alter the character, condition, form, or function of ecosystems) pose a serious threat to wildlands in California and elsewhere (Randall 1997; Vitousek et al. 1997; Richardson et al. 2000; Bossard & Randall 2007). In California's estuarine wetlands, some of the most problematic and well-known ecosystem transformers are the introduced *Spartina* species, especially *S. alterniflora* Loisel. and its hybrids (Callaway 2005; California Conservancy 2007).

Historically, the coastal plains of California have been exposed to multiple introductions for long periods of time, and consequently they support more nonnative plant species than many other parts of the state (Randall et al. 1998; Bossard & Randall 2007). Wetlands are especially vulnerable to plant invasions, particularly in coastal or urban areas that experience significant pressures from human activities (Galatowitsch et al. 1999; Ruiz et al. 2000; Callaway & Zedler 2004; Zedler & Kercher 2004). Even salt marshes, which historically have not experienced significant invasions owing to naturally high salinity levels and anaerobic conditions that inhibit establishment of most nonnative plants, are now highly invaded ecosystems (Callaway 2005; Grewell et al. 2007). Accordingly, the proximity of wetlands to large urban centers, which function as landscape sinks, facilitates multiple disturbances, alterations to hydrological regimes, and dissemination of propagules that promote the establishment of nonnative facultative wetland plants (Galatowitsch et al. 1999; Cronk & Fennessy 2001; Zedler & Kercher 2004). In southern California, expanding urbanization provides year-round sources of water from runoff and discharge of wastewaters into natural drainages, which provide direct pathways of dispersal for nonnative species spreading from uplands to wetlands at the wildland-urban interface (White & Greer 2006; Riefner & Boyd 2007).

In this paper, we provide the first documented records of *Paspalum vaginatum* Sw. (Poaceae, Panicoideae, Paniceae) for California. *Paspalum vaginatum* (seashore paspalum, saltwater couch, saltwater paspalum, siltgrass) is widely recognized as a serious invasive pest and an ecosystem transformer that has naturalized in many subtropical and tropical coastal wetland environments, often with detrimental effects to the structure and function of indigenous ecosystems (Graeme & Kendal 2001; Shaw & Allen 2003; Weber 2003; Dana et al. 2004; Siemens 2006). In order to understand the introduction and establishment of this species in southern California, we review its anthropogenic uses and invasive status worldwide, and examine its biological traits that promote invasiveness and the formation of monocultures in estuarine wetlands. Rapidly expanding populations and the formation of dense monocultures pose a serious threat to the structure, function, and biological composition of tidal marshes, sloughs, and mudflats in southern California.

Specimens Seen. The known range of *P. vaginatum* in southern California is depicted on Figure 1. Individual populations documented by voucher specimen data are as follows: **CALIFORNIA. Los Angeles Co.:** City of Malibu, Zuma Lagoon at Westward Beach Rd., UTM (NAD 83) 11S 0331858E 3765305N, elev. 3 m (10 ft), rare, mud flat with *Jaumea*, 4 Nov 2005, *Riefner 05-744* (RSA); City of Malibu, Malibu Lagoon, W lagoon, S of Pacific Coast Hwy., UTM (NAD 83) 11S 0344592E 3767052N, elev. 1 m (3 ft), common on mud flats, channel banks, and in salt marsh with *Frankenia* and *Jaumea*, highly invasive and displacing native species, 8 Jul 2006, *Riefner 06-290* (RSA); City of Malibu, Malibu Lagoon, E lagoon near Surfrider Beach, S of Pacific Coast Hwy., UTM (NAD 83) 11S 0344854E 3767212N, elev. sea level, local but widespread along inlet channel, on mud flats, and in salt marsh with *Salicornia*, 8 Jul 2006, *Riefner 06-293* (RSA); City of Carson, near Victoria Park, Dominguez Channel at Del Amo Blvd., UTM (NAD 83) 11S 0392422E 3746119N, elev. 7 m (23 ft), locally abundant, growing with *Distichlis* and *Atriplex* in saturation zone along channel, 29 Jul 2006, *Riefner 06-327* (RSA); City of Carson, Dominguez Channel, S of Del Amo Blvd. near Carson St., UTM (NAD 83) 11S 0392702E 3745799N, elev. 7 m (23 ft), widespread and well established, growing with and over *Salicornia*, *Distichlis*, and *Atriplex* in saturation zone along channel, 29 Jul 2006, *Riefner 06-330* (RSA). **Orange Co.:** City of San Juan Capistrano, Trabuco Creek, N side of Del Obispo St. at Paseo Adelento St., UTM (NAD 83) 11S 0438127E 3706763N, elev. 27 m (89 ft), uncommon, sandy streambed in shallow fresh water with *Paspalum distichum*, 14 Oct 2003, *Riefner 03-455* (RSA); City of San Juan Capistrano, Trabuco Creek, S side of Del Obispo St. at Paseo Adelento St., UTM (NAD 83) 11S 0438127E 3706763N, elev. 26 m (85 ft), uncommon, sandy streambed in shallow fresh water, 14 Oct 2003, *Riefner 03-456* (RSA); City of Mission Viejo, Oso Creek, ca. 0.5 mi N of Paseo De Colinas on Camino Capistrano, UTM (NAD 83) 11S 0437527E 3714753N, elev. 86 m (281 ft), well established and highly invasive along perennial creek in mud and shallow water discharged from a waste water treatment plant, and in saturated soil in open riparian scrub growing with *Baccharis salicifolia*, *Pulicaria paludsoa*, and *Salix lasiolepis*, 9 Jul 2005, *Riefner 05-543* (RSA); City of Mission Viejo, Oso Creek, ca. 1.4 mi N of Paseo De Colinas on Camino Capistrano, UTM (NAD 83) 11S 0437526E 3715062N, elev. 88 m (282 ft), well established and highly invasive along perennial creek in mud and shallow water discharged from a waste water treatment plant, and in saturated soil in open riparian scrub growing with *Baccharis salicifolia*, *Paspalum distichum*, and *Schoenoplectus americanus*, 9 Jul 2005, *Riefner 05-545* (RSA); City of Laguna Niguel, Aliso Creek, Alica Pwky. at Skate Park Way, UTM (NAD 83) 11S 0433416E 3713654N, elev. 46 m (151 ft), locally established in wet sand in creek with shallow fresh water,

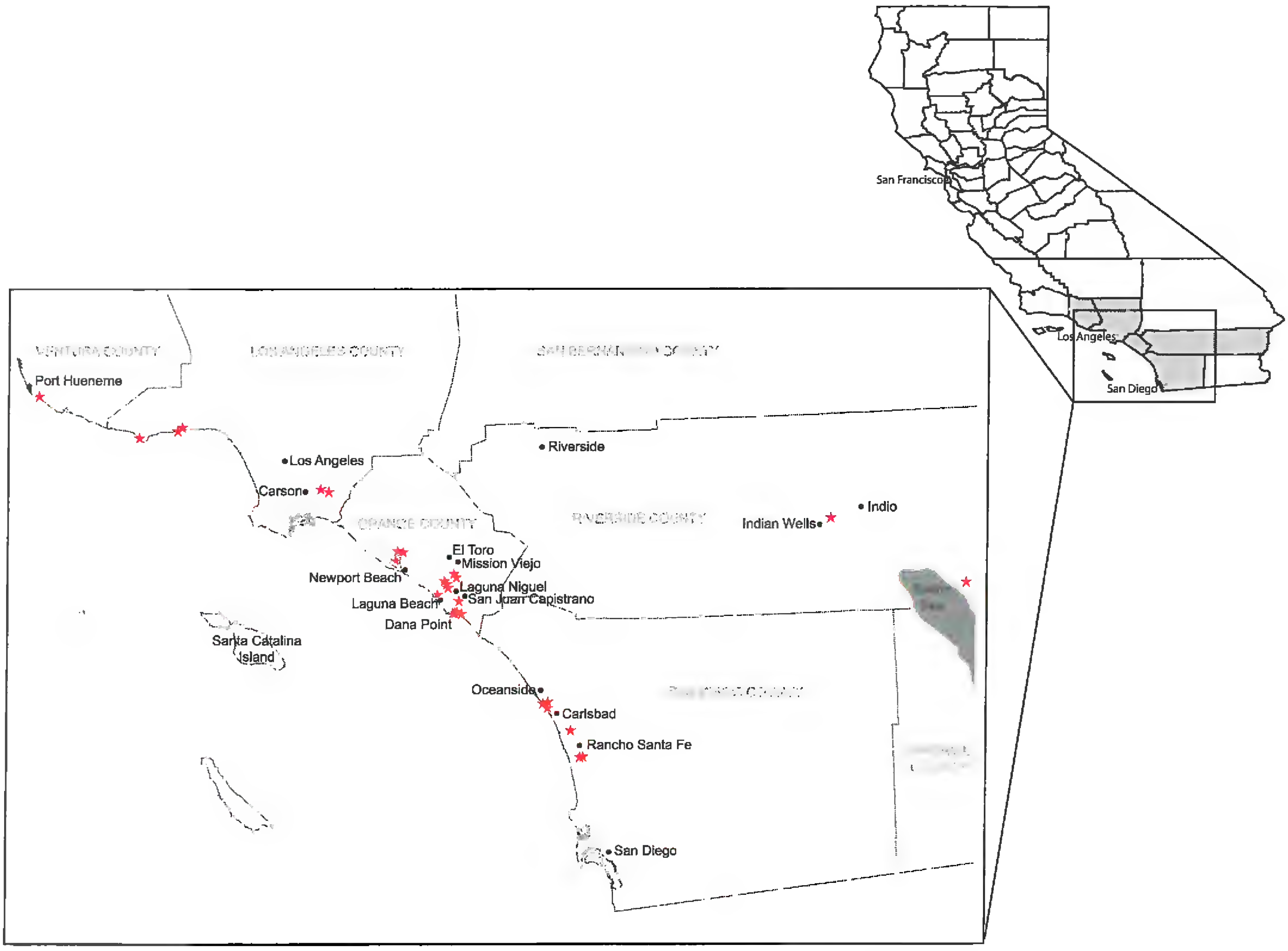

Fig. 1. Known distribution of *Paspalum vaginatum* in southern California. Individual populations documented by voucher specimens (RSA) are shown in red.

growing with *Agrostis*, *Leptochloa*, *Polypogon*, and *Typha*, 8 Jul 2007, *Riefner 07-304* (RSA); City of Newport Beach, E of Jamboree Rd. at Bayview Way, San Diego Creek at confluence with Newport Bay, UTM (NAD 83) 11S 0419719E 3723895N, elev. 6 m (20 ft), tidal wetland, widespread and well established on mud flats and in salt marsh growing with *Salicornia*, *Limonium*, and *Jaumea*, highly invasive and excluding native species, 23 Jul 2007, *Riefner 07-314* (RSA); City of Dana Point, Doheny State Beach, E side of San Juan Creek Lagoon, UTM (NAD 83) 11S 0436583E 3702748N, elev. 4 m (13 ft), locally established but invasive, many individual plants scattered on mud flats and wet sand, 17 Oct 2007, *Riefner 07-434* (RSA); City of Dana Point, Doheny State Beach, W side of San Juan Creek Lagoon, UTM (NAD 83) 11S 0436475E 3702895N, elev. 6 m (20 ft), locally common on dry banks with *Baccharis salicifolia*, and on lagoon mud flats with *Jaumea*, *Aster subulatus* var. *ligulatus*, *Baccharis salicifolia*, *Distichlis*, and *Typha*, 17 Oct 2007, *Riefner 07-436* (RSA); City of Dana Point, Dana Point Harbor, Dana Point Harbor Dr. near Park Lantern Dr., UTM (NAD 83) 11S 0436040E 3702905N, elev. 4 m (13 ft), locally common and invasive, urban creek and adjacent sandy flats with *Cynodon*, *Cyperus involucratus*, *Ehrharta erecta*, *Paspalum dilatatum*, and *Typha*, 17 Oct 2007, *Riefner 07-437* (RSA); City of Dana Point, Doheny State Beach, Dana Point Harbor Dr. near Puerto Pl., UTM (NAD 83) 11S 0435964E 3702721N, elev. 10 m (33 ft), local, sand dune swale with *Distichlis* and *Juncus acutus*, 17 Oct 2007, *Riefner 07-439* (RSA); City of Laguna Niguel, Laguna Niguel Regional Park, vicinity of La Paz Rd. at Aliso Creek, UTM (NAD 83) 11S 0434146E 3712609N, elev. 64 m (210 ft), locally established on creek bank with *Atriplex prostrata* and *Typha*, 26 Oct 2007, *Riefner 07-452* (RSA); City of Laguna Niguel, vicinity of La Paz Rd. at Kings Rd., UTM (NAD 83) 11S 0434619E 3711316N, elev. 64 m (210 ft), locally established in concrete channel draining water-reclamation facility, growing with *Atriplex prostrata* and *Typha*, 26 Oct 2007, *Riefner 07-459* (RSA); City of Newport Beach, North Star Beach, north shore of Newport Bay near North Star Ln., UTM (NAD 83) 11S 0417162E 3721028N, elev. 9 m (30 ft), rare on tidal channel bank and in salt marsh, growing near population of *Cordylanthus mollis* subsp. *maritimus*, 26 Oct 2007, *Riefner 07-461* (RSA); City of Laguna Beach, Aliso Creek at Pacific Coast Hwy., UTM (NAD 83) 11S 0430150E 3708320N, elev. ca. 9 m (30 ft), abundant and invasive on creek banks in tidal waters with *Pulicaria* and *Jaumea*, 13 Jan 2008, *Riefner 08-4* (RSA); City of Newport Beach, San Diego Creek at Hwy. 73, E of Jamboree Rd., UTM (NAD 83) 11S 0419906E 3723854N, elev. ca. 6 m (20 ft), locally established on disturbed creek bank in tidal waters, growing with *Cotula* and *Schoenoplectus*, 13 Jan 2008, *Riefner 08-9* (RSA). **Riverside Co.:** Salton Sink, Dos Palmas Oasis, managed ponds near The Nature Conservancy preserve, 33°30.04'N 115°49.9'W, elev. –37 m (–121 ft), wet soil and shallow water, 4 Dec 1994, *Sanders et al. 15885* (RSA) [originally det. as *Paspalum distichum*; annotated Nov. 2007]; Indian Wells, tributary to Whitewater River, Hwy. 111 near Happy Point, UTM (NAD 83) 11S 0564872E 3730987N, elev. ca. 20 m (66 ft),

uncommon in wet sand along slow-moving waters of urban creek, growing with *Scirpus robustus*, *Leptochloa fusca* subsp. *uninervia*, and *Eclipta*, 7 Aug 2005, *Riefner 05-596* (RSA). **San Diego Co.:** City of Rancho Santa Fe, La Orilla St. at El Camino Real, San Elijo Lagoon, UTM (NAD 83) 11S 477707E 3652459N, elev. 12 m (39 ft), well established on marsh banks and in shallow water with *Ludwigia peploides* subsp. *peploides*, 8 Sep 2002, *Riefner 02-224* (RSA); City of Rancho Santa Fe, La Orilla St. ca. 0.4 mi E of El Camino Real, UTM (NAD 83) 11S 0478231E 3652819N, elev. 21 m (69 ft), well established but local on creek banks and in open marsh, growing with *Aster subulatus* var. *ligulatus*, *Distichlis*, and *Salicornia*, 8 Sep 2002, *Riefner 02-224* (RSA); City of Oceanside, Loma Alta Slough, Buccaneer Park, Pacific St. at Morse St., UTM (NAD 83) 11S 0465660E 3671043N, elev. 1 m (3 ft), well established but local in moist sand and on creek banks, growing with *Distichlis*, *Salicornia*, *Schoenoplectus*, *Jaumea*, and *Atriplex prostrata*, 8 Sep 2002, *Riefner 02-221* (RSA) [originally det. as *Paspalum distichum*; annotated Oct. 2003]; same locality, widespread, highly invasive and excluding native species, 5 Oct 2007, *Riefner 07-420* (RSA); City of Oceanside, Loma Alta Creek at Pacific Coast Hwy., UTM (NAD 83) 11S 0465836E 3671307N, elev. 13 m (43 ft), locally established in creek bed in wet sand near flowing water, growing with *Leptochloa*, *Schoenoplectus californicus*, and *Typha*, 5 Oct 2007, *Riefner 07-420* (RSA); City of Oceanside, Buena Vista Lagoon, Rue des Chateaux at Ocean St., UTM (NAD 83) 11S 0466593E 3669614N, elev. 1 m (3 ft), locally established on mud flat and in disturbed salt marsh, growing with *Jaumea*, *Juncus acutus*, and *Tamarix*, 15 Oct 2007, *Riefner 07-429* (RSA); City of Carlsbad, Batiquitos Lagoon, vicinity of Arenal Rd. at Columbine Dr., UTM (NAD 83) 11S 0474831E 3661679N, elev. 5 m (16 ft), rare, invading *Jaumea* marsh, 15 Oct 2007, *Riefner 07-432* (RSA). **Ventura Co.:** City of Point Hueneme, Bubbling Springs Greenbelt, vicinity of Surfside Dr. and Port Hueneme Dr., UTM (NAD 83) 11S 0297999E 3780473N, elev. 3 m (10 ft), locally common on creek banks, and spreading to shallow water and in marsh with *Ludwigia*, *Typha*, and *Schoenoplectus*, 8 Jul 2006, *Riefner 06-280* (RSA).

PREVIOUS KNOWLEDGE

Distribution.—*Paspalum vaginatum* is a perennial grass documented from warm, coastal regions around the world, including southwest and southeast Europe, tropical Africa, temperate and tropical Asia (Arabia, China, India, Malaysia), Australia, New Zealand, French Polynesia, the Galápagos Islands, Hawaii, and other Pacific Islands, the Caribbean, Central and South America, and the Atlantic and Gulf Coasts of the United States and Mexico in North America (Waterhouse 1997; Allen & Hall 2003; Zuloaga et al. 2003; Clayton et al. 2006). Its exact native range, which is centered in the tropical and subtropical regions of the New World, remains uncertain (Chase 1929; Wagner et al. 1999; Edgar & Connor 2000; Weber 2003). In the United States, *P. vaginatum* occurs from North Carolina to Florida, west in the Gulf States to Texas, and in New Mexico, but was not previously reported for California (Webster 1993; Allen & Hall 2003; DiTomaso & Healy 2007; USDA 2007; Jepson Flora Project 2008).

Across its range, and outside of cultivation, *P. vaginatum* occupies coastal salt and brackish water marshes, shallow-water lagoons and tidal channels, mangroves, coastal shrublands, dunes and beaches, summer-moist saltpans, wet pastures, and freshwater riparian and floodplain habitats in many warm temperate, subtropical, and tropical environments (Skerman & Riveros 1990; Stutzenbaker 1999; Wagner et al. 1999; Edgar & Connor 2000; Filigheddu et al. 2001; Allen & Hall 2003; Shaw & Allen 2003; Dana et al. 2004; Siemens 2006).

Anthropogenic Uses and Worldwide Introductions.—*Paspalum vaginatum* has numerous anthropogenic uses that have transported it to many countries around the world, and eventually to southern California. Historically, it was used as bedding in trade ships that sailed between Africa, North and South America, Central America, and the Caribbean Islands during the 1700s and 1800s (Duncan & Carrow 1999). *Paspalum vaginatum* has also been used widely for rehabilitation of salt-affected lands, stabilization of sand dunes and dredge materials, restoration of coastal wetlands, and forage for livestock (Leithead et al. 1971; OIC 1990; Vargas 1995; NRCS 1999; Loch & Lees 2001; Barrett-Lennard et al. 2003; Fontenot 2007).

As water shortages continue to escalate worldwide, increased use of saline water or poor-quality reclaimed effluent waters for turf landscape irrigation is necessary (Snow 2001). The systematic development and cultivation of varieties (cultivars) of turf grasses with improved tolerance to saline soils and low-quality irrigation waters, including *P. vaginatum*, are playing a central role in the turf grass industry (Henry 1981; Hall 1994; Brown et al. 1998; Carrow & Duncan 1998; Duncan 2003; Marcum 2004). To meet the demands of water conservation and expanding recreational needs, *P. vaginatum* is now grown on golf courses in Asia (including Malaysia, Indonesia, and the Philippines), South Africa, the Middle East, Sardinia, New Zealand, South America, Hawaii, the Caribbean Islands, and across the southern United States (Duncan & Carrow 1999; Beard 2002). *Paspalum vaginatum* is also used as a ground cover in gardens, and new cultivars are

highly promoted for lawns in the southern United States (USDA Zones 7–10), Australia, Hawaii, and elsewhere (Duncan & Carrow 1999; Rushing 2006; Christians et al. 2007; Tukey 2007).

Environmental Tolerances Create a Competitive Advantage.—*Paspalum vaginatum* has broad ecological tolerances and life history traits that aid its widespread establishment and utility to land and resource managers worldwide. It is an ecologically aggressive, rhizomatous and stoloniferous mat-forming perennial grass that often forms extensive colonies (Hitchcock 1951; Weber 2003). It roots well in sand, clay, silt or mucky soils in acidic or alkaline conditions, is tolerant of waterlogged and highly saline soils, prospers in low fertility soils and poor-quality effluent waters used for irrigation, is highly tolerant of mechanical mowing and heavy livestock grazing, has high shoot density for effective soil stabilization, develops a thick low-maintenance turf tolerant of foot traffic and wear, and is not readily susceptible to drought or pathogens (Duncan 1999; Duncan & Carrow 1999; Loch & Lees 2001; Barrett-Lennard et al. 2003; Lee et al. 2004a,b; Fontenot 2007). Therefore, its rapid growth, abundant propagules (in this case rhizome and stolon fragments), and broad environmental tolerances are important characteristics typical of an "ideal weed" (Sakai et al. 2001). In a given environment, these characteristics often confer an advantage to a nonnative species relative to indigenous species (Barney & DiTomaso 2008).

Invasive Status Worldwide.—*Paspalum vaginatum* is well known for its aggressive behavior and its ability to alter wetland ecosystem function (Weber 2003). It is an early and effective colonizer of disturbed, bare or ephemeral soil deposits, and once established it can exclude indigenous species recruitment for many years (Shaw & Allen 2003). *Paspalum vaginatum* is, however, self-incompatible, rarely produces viable seed in significant quantity, and therefore, must be propagated vegetatively (Hall 1994; Duncan & Carrow 1999). However, it would be careless to conclude that species lacking sexual reproduction cannot become serious invaders; giant reed (*Arundo donax* L.) is a classic example of a sterile but highly invasive plant of southern California's riparian habitats (Bossard et al. 2000; Barney & DiTomaso 2008).

Outside of cultivation, vegetative reproduction of *P. vaginatum* would be possible through animal grazing and other natural physical regimes that would disturb and transport rhizomes and stolons (Graeme & Kendal 2001). *Paspalum vaginatum* is apparently dispersed primarily by water when pieces of stolon or rhizome are carried often long distances by streams. These vegetative fragments root easily, forming new plants that start new infestations (Weber 2003). Estuarine mudflats, shallow brackish lagoons or tidal creeks, and gaps in disturbed wetlands or scoured streambeds that are not readily colonized by indigenous species are highly vulnerable to invasion (Filigheddu et al. 2001; Shaw & Allen 2003; Siemens 2006). Importantly, *P. vaginatum* and its impacts on the function of native estuarine ecosystems are significant and comparable to the well-documented invasions by nonnative *Spartina* species (Graeme & Kendal 2001; Allen & Shaw 2003; Dana et al. 2004; Siemens 2006).

In New Zealand estuaries, and much like the ecological impacts effected by introduced *Spartina* species, *P. vaginatum* transforms the composition and structure of indigenous vegetation by growing over and displacing low-stature species, endangering populations of threatened species, altering fish spawning and feeding grounds, prohibiting burrowing fauna and reducing access to feeding sites and roosting by shore birds due to its high shoot and root density, and altering estuarine hydrology by accumulating sediments (Graeme & Kendal 2001; Shaw & Allen 2003).

Similar negative effects in brackish wetlands have been documented in Spain, where *P. vaginatum* displaces halophytes and alters the composition and structure of native communities, promotes accumulation of sediments and organic detritus, and alters hydrological and nutrient regimes (Dana et al. 2004). Accordingly, *P. vaginatum* has been classified as "dangerous" (a species causing ecological damage or alteration to natural ecosystems) (Dana et al. 2007). *Paspalum vaginatum* has also been classified as invasive in Portugal (Domingues de Almeida & Freitas 2006).

In the Galápagos Islands, Ecuador, *P. vaginatum* stands out as a special case. It has aggressively invaded disturbed and natural wetlands where it replaces native plants, and affects water movement and soil moisture content (Vargas 1995; Gravez et al. 2004; Guézou et al. 2007). *Paspalum vaginatum* has also successfully

invaded many lagoons, threatening these ecosystems and their globally significant avifaunal biodiversity. Quantitative investigations have determined that *P. vaginatum* infestations are responsible for degrading fiddler crab habitat, and for altering foraging habitat of aquatic birds by decreasing surface water availability during feeding (Siemens 2006). Overall, these infestations facilitate a shift from an aquatic to a more terrestrial invertebrate community, thereby affecting food availability for native fauna foraging in and around lagoons (Siemens 2006). Accordingly, its control and eradication are necessary.in order to maintain the status of the Galápagos Islands lagoons as a Ramsar Internationally Important Wetland (Siemens 2006).

In South Africa, H§fliger & Scholz (1980) documented similar negative affects to native community functions, including competition for space, light, water, and nutrients, replacement of native vegetation, obstruction of water flow, and contaminant seed loading. Further, the invasion of *P. vaginatum* and other nonnative grasses has rendered the sand and mudflats of the Wilderness Lakes Wetland (designated a Ramsar site) unsuitable for wading birds (Randall & Russell 1995).

Paspalum vaginatum is also invasive and has been classified as a "significant environmental weed" in Australia (Randall 2007). It is also invasive in the Hawaiian Islands and the Marshall Islands (Wagner et al. 1999; Whistler & Steele 1999; Vander Velde 2003). Accordingly, PIER (2007) has ranked *P. vaginatum* as a "high risk" invasive species.

SIGNIFICANCE IN SOUTHERN CALIFORNIA

Introduction, Dispersal, and Naturalization.—These naturalized populations represent the first documented records of *P. vaginatum* for California (Webster 1993; Allen & Hall 2003; USDA 2007). *Paspalum vaginatum* has also not been included in major publications on nonnative species established in California (Bossard et al. 2000; Hrusa et al. 2002; DiTomaso & Healy 2003; Bossard & Randall 2007; DiTomaso & Healy 2007; Grewell et al. 2007). Thus far, *P. vaginatum* has not been of concern in southern California (Roberts 1998; Roberts et al. 2004; Rebman & Simpson 2006; Clarke et al. 2007; Riefner & Boyd 2007).

Biologists often have difficulty tracing the source of nonnative organisms and verifying their accidental versus intentional human transport across natural boundaries. However, the arrival of *P. vaginatum* in California is most likely the result of purposeful introductions, presumably for soil stabilization and habitat enhancement projects or more likely for cultivation of turf grass for lawns, parks, and golf courses. Native in the southeastern United States, *P. vaginatum* has been used for restoration of coastal wetlands, stabilization of dunes, banks, and dredge materials in the Gulf States (Duncan & Carrow 1999; NRCS 1999; Fontenot 2007). Accordingly, it may have been introduced for enhancement or restoration of salt marsh habitats in southern California, but we have not been able to confirm this.

However, *P. vaginatum* was introduced to southern California for cultivation as a turf grass during the 1970s and 1980s for research at the University of California South Coast Field Station in El Toro, Orange County, and for commercial production in Indio, Riverside County. It was also planted for turf grass in Laguna Niguel, Orange County, and at Rancho Santa Fe, San Diego County (Henry et al. 1979; Duncan & Carrow 1999). As documented by herbarium records (*Sanders et al. 15885*, RSA; originally identified as *P. distichum*), the earliest escaped and naturalized plants were collected in 1994 near the Salton Sea, Riverside County (Fig. 1). The senior author also made observations of *P. vaginatum* in 1994 (originally identified as *P. distichum* and not collected) at Doheny State Beach, City of Dana Point, Orange County, during surveys conducted for California State Parks (Fig. 1). Species beginning to escape cultivation receive little attention, largely because of the difficulty in identifying and locating them before they become established in native communities. Time lags in plant invasions, a phase when plants are difficult to document during early dispersal, then exponential growth, naturalization in native communities, and subsequent spread describes a typical invasion scenario (Sakai et al. 2001; Schierenbeck et al. 2007). In the case of *P. vaginatum*, plants escaping cultivation from sites in El Toro and Laguna Niguel, Orange County, to native habitats on the coast at Dana Point, Orange County, and from inland sites at Indio to near the Salton Sea in Riverside County, perhaps during the 1990s, appears to be a logical scenario for southern California (Fig. 1).

For this reason, we believe turf plantings may be the most likely source of propagules that dispersed from irrigated urban landscapes downstream to native plant wetland communities. Although its reproduction outside of cultivation and dispersal mechanisms are not well understood, *P. vaginatum* may have been spread vegetatively by animals, carried by mechanized landscape equipment to new sites, or rhizome and stolon fragments may have been dispersed by water during storm events from turf plantings in the uplands into urban drainages and then downstream to native wetland communities.

Paspalum vaginatum is now widely naturalized in southern California's coastal wetlands and at inland habitats near the Salton Sea (Fig. 1). It is most common in estuarine wetlands where it can form monocultures on mudflats, tidal marshes, and shores of estuary lagoons (Fig. 2), or along tidal creeks and sloughs (Fig. 3). Bare soils of tidal mudflats (Fig. 4) and wet sand of disturbed streambeds (Fig. 5) appear to be highly vulnerable to colonization. *Paspalum vaginatum* also grows in many non-saline wetland habitats, including disturbed riparian scrub and slow-moving waters of urban creeks in coastal and desert regions. However, *P. vaginatum* is unlikely to form extensive monocultures or survive long-term competition from large, fast-growing plants and shrubs outside of saline environments.

Urbanization and Wetland Sinks.—*Paspalum vaginatum* is one of many subtropical and tropical non-native plants now established and spreading in southern California. Expanding urbanization has fragmented natural habitats, encouraging nonnative plants cultivated in cities to move easily from human-maintained landscapes to native communities (Vitousek et al. 1996; Cronk & Fennessy 2001). In urban environments, wetlands often accumulate debris and sediments, and receive floodwaters that supply resources (nutrient enrichment, elevated levels of light following flood scour) that may accelerate the growth of opportunistic nonnative plants and facilitate invasion of sunny gaps in the vegetation (Davis et al. 2000; Zedler & Kercher 2004). In addition, hydrological and hydrogeomorphic alterations, accelerated erosion, and other anthropogenic disturbances to wetland and riparian habitats have created numerous opportunities for invasion by nonnative hydrophytes (Newman et al. 1996; Tickner at al. 2001; Werner & Zedler 2002).

Historically, summer drought and the seasonal nature of stream flows in coastal southern California have acted as a barrier to colonization by nonnative facultative wetland plants in the wildland-urban interface (Brigham 2007; Riefner & Boyd 2007). Increased moisture availability in urban environments, and a shift from ephemeral to perennial stream flows owing to waste water discharge into natural drainages in an otherwise summer-dry climate have facilitated the dispersal of these species throughout urbanized southern California (Greer & Stow 2003; Riefner & Boyd 2007).

Biological Traits Promoting Invasiveness in Estuarine Wetlands.—Many wetland plant invasions can be explained by the ecological requirements and attributes of the potentially invasive plant species and the local environmental opportunities afforded by anthropogenic disturbances (flooding, nutrients, propagules, sediments) that may promote invasion and the formation of monocultures in wetland sinks (Werner & Zedler 2002; Kercher & Zedler 2004; Zedler & Kercher 2004). In addition, the selection and breeding for horticultural or agronomic purposes of an individual species, its cultivation in seemingly naïve environments, followed by escape and naturalization, often with detrimental effects to sensitive ecosystems, describes a scenario typical of many invasive plants introduced and now established in the United States (Reichard & White 2001).

Paspalum vaginatum cultivars with improved salt-tolerant characteristics have been developed and are now used widely in the turf grass industry (Lee et al. 2004a,b; Duncan & Carrow 1999; Duncan 2003). *Paspalum vaginatum* is one of the most saline-tolerant turf species available, with ecotypes exhibiting high-vigor root and shoot growth at high salinity levels (Carrow & Duncan 1998; Beard 2002; Lee et al. 2005). Additionally, cultivars have also been developed and evaluated for improved growth rate and transplant survival for restoration and soil stabilization of brackish shorelines, dunes, mudflats, and dredge materials in the Gulf Coast region of the southern United States (Duncan & Carrow 1999; NRCS 1999; Fontenot 2007).

Fig. 2. *Paspalum vaginatum* is often highly invasive in estuarine wetlands and may form monocultures in tidal marshes, on mudflats, and along shores of estuary lagoons. Photograph taken at Malibu Lagoon, Los Angeles County.

Fig. 3. Marsh habitats and sandy flats along brackish tidal channels and sloughs also support monocultures of *P. vaginatum* that displace native hydrophytes. Photograph taken at Loma Alta Slough, Oceanside, San Diego County.

Fig. 4. Mudflats in tidal wetlands are highly vulnerable to invasions by *P. vaginatum*. Photograph taken at San Diego Creek near confluence of Newport Bay, Newport Beach, Orange County.

Fig. 5. Disturbed urban streambeds characterized by heavy sediment deposition are rapidly colonized by *P. vaginatum*. Rhizome and stolon fragments, spreading from upland landscapes to drainages during rainstorms, start new infestations and act as stepping-stones that facilitate the invasive spread downstream to estuarine wetlands. Photograph taken at Loma Alta Creek, Oceanside, San Diego County.

Table 1. Attributes of *P. vaginatum* that promote invasive behavior in urban wetlands and its ability to form monocultures in estuarine wetlands in southern California (based on the literature and personal observations).

Opportunity or Wetland Niche Open to Invasion	Adaptations and Attributes That Promote Invasiveness and the Formation of Monocultures
Unvegetated mudflats	Inundation tolerance, aggressive colonization, lack of competition from native hydrophytes
Waterlogged and anoxic soils	Aerenchyma in roots
Alterations to hydroperiod, fluctuating water depth, and shallow water	Broad ecological tolerance, rhizomes and stolons that float and grow out into water, adventitious roots, and rapid growth
Saline soils	High salt tolerance, sustained vigor and shoot growth in salt-affected sites
Flooding, nutrient influx, and sediment deposition	Rhizome and stolon fragments dispersed by water, aggressive colonization and establishment, dense persistent rhizome mats, and lack of competition from native hydrophytes
Summer-wet urban drainages	Warm-season growth with C_4 pathway, wide pH tolerance and adaptation to diverse soil types
Canopy gaps	High light requirements, aggressive colonization, and lack of competition from fast-growing native hydrophytes

Accordingly, *P. vaginatum* cultivars could become invasive, and might have significant detrimental effects to native estuarine ecosystems if they escape from urban environments or if they are used in restorations outside the native range of the species, including the southwestern United States. The biological adaptations and attributes of *P. vaginatum* that promote its invasive behavior associated with anthropogenic disturbance in urban wetlands, and its ability to form monocultures in native estuarine wetlands are summarized in Table 1.

Impacts to the Environment.—Our field observations indicate *P. vaginatum* is a threat to the ecological function of estuarine wetlands in southern California. We currently lack experimental data to substantiate the changes to wetland composition and structure that we have observed. However, strong anecdotal evidence and quantitative data gathered in other countries provide sufficient baseline information indicating its impacts to native ecosystems may be significant and comparable to the well-documented invasions by introduced *Spartina* species (Graeme & Kendal 2001; Shaw & Allen 2003; Dana et al. 2004; Siemens 2006).

Invasions of *Spartina* species, especially *S. alterniflora* and its hybrids, have engineered the alteration of habitats critical to endangered species, conversion of tidal mudflats to meadow, changes to creek morphology and hydrological regimes, failure of local wetland restoration projects, and local extinctions of the native California cord grass (*Spartina foliosa* Trin.) in the San Francisco Estuary (Ayres et al. 2004; Callaway 2005; Strong & Ayres 2005; California Conservancy 2007; Grewell et al. 2007). Comparisons of the environmental impacts of introduced *Spartina* species versus *P. vaginatum* are summarized in Table 2.

DISCUSSION

Wetlands are uniquely important natural resources that are highly vulnerable and threatened in southern California (Ferren & Fiedler 1993). Poor historical documentation, rapidly expanding urbanization, habitat fragmentation, and poorly coordinated conservation programs have resulted in the long-term, unmitigated loss and degradation of wetland resources, which are proportionally higher in California than in other parts of the United States (Dahl 1990; Grewell et al. 2007). To compound historic losses, wetland invasions by nonnative species also threaten native biodiversity and ecosystem function, which may soon surpass habitat loss as the main cause of environmental degradation (Chapin et al. 2000; Grewell et al. 2007).

TABLE 2. Comparison of impacts to estuarine wetland composition and structure documented for introduced *Spartina* species in the San Francisco Estuary, northern California, versus observed or potential impacts of *P. vaginatum* in southern California's estuarine wetlands.

Impacts of *Spartina* Species: San Francisco Estuary	Impacts of *Paspalum vaginatum*: Southern California Estuarine Wetlands
Impacts to sensitive species: competes for space with the federally listed *Cordylanthus mollis* subsp. *mollis*	**Impacts to sensitive species:** competes for space with the federally and state-listed *Cordylanthus maritimus* subsp. *maritimus*
chokes channels used by the endangered California clapper rail to forage, and displaces pickle weed marsh of the endangered salt marsh harvest mouse	insufficient information available for potential impacts to listed animal species
	potentially competes with, grows over, or inhibits germination of other sensitive plants: *Eleocharis parvula*, *Lasthenia glabrata* subsp. *coulteri*, and *Suaeda esteroa*
Converts tidal mudflats to meadow or marsh: coalesces to form cord grass meadows	**Converts tidal mudflats or sand flats to meadow or marsh: dense mats exclude or smother low-stature halophytes**
accretes and stabilizes sediment among dense shoots, which increases the elevation of the mud flat for further colonization	stabilizes and possibly accretes sediment and organic detritus among dense shoots, to stolons, and rhizomes for further colonization
	high shoot, rhizome, and stolon density potentially excludes or could alter composition of burrowing fauna
Loss of shorebird foraging habitat: fills in the open mud of channels and sloughs, altering marsh hydrology	**Loss of shorebird foraging habitat:** colonizes mudflats, tidal creek channels, and shallow lagoon waters, which could become unsuitable for wading birds
Loss of critical channel habitat: alters marsh hydrology and channel habitat	**Loss of critical channel habitat:** insufficient information available
Local extinction of the native California cord grass (*S. foliosa*): conversion of native California cord grass marsh to dense swards of *S. alterniflora* hybrids	**Local exclusion of native halophytes:** grows over and smothers low-stature species of *Atriplex*, *Batis*, *Cressa*, *Distichlis*, *Frankenia*, *Isolepis*, *Jaumea*, *Limonium*, *Monanthochloe*, *Salicornia*, *Spergularia*, and *Triglochin*
Failure of wetland restoration project objectives: displaces and excludes recruitment of native species	**Failure of wetland restoration project objectives:** potentially displaces and excludes recruitment of native species

Paspalum vaginatum is a highly aggressive invasive species that poses a serious threat to wetland diversity by transforming the physical structure and biological composition of tidal marshes and mudflats in southern California. Because the use of *P. vaginatum* will probably increase in turf grass landscapes across urbanizing southern California, it is unlikely that the species will decline. In fact, *P. vaginatum* will most likely spread to new regions, which points to an immediate need to control or eradicate expanding infestations.

Management and research programs have been developed to monitor and restore *P. vaginatum*-affected wetlands in other countries (Graeme & Kendal 2001). Potential strategies and resource management topics relevant for urbanized southern California are:

1) Create awareness and educate biologists, field researchers, and resource agencies regarding the invasive behavior of *P. vaginatum*;

2) Add *P. vaginatum* to the California Invasive Plant Council list of plants of greatest ecological concern (severe ecological impacts on physical processes, plant and animal communities, and vegetation structure);
3) Expand field surveys to determine the complete distribution and abundance in native habitats, quantify expanding use in urban landscapes, and determine if it is used in restorations;
4) Assign *P. vaginatum* an obligate wetland indicator status (OBL, found >99% of the time in wetlands) for California (Region 0) on the National List of Plant Species that Occur in Wetlands to aid wetland delineations;
5) Identify and monitor adverse ecological changes to wetland ecosystems and potential impacts to sensitive floral and faunal elements;
6) Develop habitat- and region-specific control programs;
7) Conduct ecological risk assessments of potential control techniques to avoid secondary impacts to sensitive resources.

The introduction and naturalization of *P. vaginatum* demonstrates the urgent need to implement detailed floristic monitoring of wetland communities in southern California's rapidly urbanizing communities. Early detection of new invasive plants would likely minimize their impacts on biodiversity and ecosystem functions, and reduce the high cost of control and eradication. Declines in biodiversity of wetland ecosystems in urbanized environments are becoming a major concern to resource managers, especially in California, which has the highest number of wildland-urban interface housing units (and associated parks, lawns, recreational landscapes planted with turf grass) in the United States (McKinney 2002; Radeloff et al. 2005; Schwartz et al. 2006). Accordingly, the widespread utility of *P. vaginatum* for turf landscapes, and potential use in wetland restorations, may require the participation of agronomists, biologists, conservation groups, and local and federal government resource agencies where wetland biodiversity and conservation objectives potentially conflict with urban landscape management practices in southern California.

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